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TAXONOMY AND DISTRIBUTION OF THE GENUS SPARTINA[1]

David George Mobberley[2]

INTRODUCTION

The genus Spartina presents a number of taxonomic problems. Contemporary authors are not in substantial agreement in their treatment of its specific and infraspecific taxa and no one author is wholly in accord with another. Criteria heretofore proposed for separating various taxa are vague and often inconsistent, particularly for infraspecific taxa. Consequently, the accurate identification of a great number of specimens is difficult. The present investigation redefines the limits of a number of species, develops keys to the included taxa, determines geographic variability within the species and compiles evidence in support of a theory of hybrid origin for several of the species.

Recent trends in taxonomy emphasize the examination and critical evaluation of a large number of specimens of any given taxon collected throughout its geographic range. The genus Spartina is admirably suited to this type of investigation because most of the species are geographically distributed along a rather narrow belt of land bordering the Atlantic Ocean and adjacent waters in certain regions of both hemispheres. This feature, coupled with its abundance, often in large, dense, pure stands, makes it an attractive genus for study.

As first conceived, the scope of the present problem was limited to the species of Spartina occurring in North America, but several facets of the problem of nomenclature demanded an examination of specimens of South American and Old World species as well. As a consequence, all the known infrageneric taxa were included. Although only the species of eastern North America were observed under field conditions and collected in quantity, sufficient western and extra-North American material was made available by loans to allow a study of the entire genus.

HISTORICAL

The genus Spartina was placed in the tribe Chlorideae of the family Gramineae by Kunth (1829). Trinius (1840) considered the genus more appropriately placed in the Agrostideae, owing to the presence of one-flowered spikelets. Steudel (1855), following Kunth, included the genus with the Chlorideae, doubtless having considered the one-sided disposition of spikelets on the spikes of greater taxonomic significance than the one-flowered spikelets.

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Bentham (1881) transferred the genus to the Chamaeraphis group of the tribe Paniceae on the grounds that the spikelet contained but a single perfect floret and that the pedicel of the spikelet articulated below the glumes. Because these conditions were not found elsewhere in the Chlorideae, the placement of Spartina in this tribe was, according to Bentham, incorrect. Scribner (1883) held that Spartina was properly placed in the Chlorideae. He countered Bentham's proposal with the argument that articulation of the pedicel below the glumes seemed insufficient reason for the transfer, especially so in view of the fact that Bentham had overlooked the position of articulation in certain genera of tribes other than the Chlorideae. Most recent American and European authors have not subscribed to Bentham's disposition of the genus but are in agreement with Scribner. Hackel (1890), Parodi (1919), Bews (1929), Hitchcock (1935), Swallen (1939), Hutchinson (1944), and Chase (1950) all placed Spartina in the Chlorideae, usually placed in the subfamily Festucoideae.

Prat (1936), on the basis of epidermal cell structure and foliar anatomy, placed the Chlorideae and its included genus Spartina in the Chloridoideae subgroup of the subfamily Panicoideae.

In an abrupt departure from the more widely accepted procedure of including Spartina in the Chlorideae, Clapham, Tutin and Warburg (1952) placed the genus by itself in the tribe Spartineae which they held to be separable from the Chlorideae on the basis of its one-flowered spikelets.

Linnaeus (1753) included Dactylis cynosuroides and its variety β in the genus Dactylis. Dactylis cynosuroides is now placed in the genus Spartina as S. cynosuroides. During the latter part of the eighteenth century, several additional species were described under Dactylis by Loefling (1758), Curtis (1787), Walter (1788), and Aiton (1789).

Schreber (1789) erected the genus Spartina but cited no species. Gmelin (1791) listed Spartina Schreb. and included a single species, S. schreberi, but did not accompany the epithet with a description. No reference was made to an earlier epithet nor was any locality given. Roth (1806) seems to have been the first to connect the spartinoid segment of Dactylis L. with Spartina Schreb.

In the early part of the nineteenth century a number of authors published short systematic lists of the species of Spartina then known. Among these were Roth (1806), Willdenow (1809), Beauvois (1812), Muhlenberg (1817), Link (1820), and Kunth (1829, 1833). Descriptions of new species appeared in several of these works. Muhlenberg's list was restricted to the species occurring in North America.

Other systematic accounts of the species were published about the same time under the genera Trachynotia (Michaux, 1803) and Limnetis (Richard in Persoon, 1807; Nuttall, 1818). The works of Michaux and Nuttall were limited to species occurring in North America.

What seems to have been the first comprehensive compilation of binomials appeared from the pen of Trinius (1840), who included six species with synonyms. Three new species were described. Subsequently, Steudel (1855) in his extensive treatment of the grasses listed twenty-three Spartina binomials, and gave descriptions for all but two of them. Many of the names had been included in the synonomy given by Trinius.

Merrill (1902) published the first monograph of the genus Spartina,

the treatment being restricted to the North American species. Nine species, one of which was new, were included. Subsequent rearrangement of species limits and nomenclatural changes by Hitchcock (1906, 1935) and Fernald (1916, 1947) have superseded many of Merrill's taxonomic conclusions.

Later systematic surveys of species of Spartina occurring in North America and the United States were prepared by Hitchcock (1935), Swallen (1939), and Chase (1950). These treatments list eight or nine species, provide keys to the species and append considerable synonomy. However, no evidence is offered to support the reduction of names to synonyms.

Species admitted to these systematic lists were S. alterniflora, S. bakeri, S. cynosuroides, S. patens, and S. spartinae of the Atlantic and Gulf coastal plains, S. foliosa of the coastal marshes of California, S. pectinata of the northern and western United States, and S. gracilis of the western plains and mountains. Some dispute had arisen over the disposition of S. caespitosa of the New England and Middle Atlantic seaboard. Hitchcock (1935) regarded it as a variety of S. patens while Swallen (1939) and Chase (1950) recognized it as a distinct species.

Publications dealing specifically with the South American species of Spartina include papers by Arechavaleta (1896) and Parodi (1919, 1937). The most comprehensive treatment was that of Parodi (1919) in which he listed five species occurring along the Atlantic seaboard in Argentina. These were Spartina alterniflora, S. ciliata, S. densiflora, S. montevidensis, and S. patagonica. A sixth species, S. argentinensis, from the inland region of Santa Fe province, Argentina, was described as new. Parodi included descriptions of the species, notes on habitats and a key.

A more recent monographic study of the genus is that of Saint-Yves (1932). The treatment is world-wide in scope. He stated that the genus was divisible into two distinct groups (Polychlorophyllae and Oligochlorophyllae) on the basis of the amount of chlorophyllous tissue within the prominent ribs on the adaxial surface of the leaf blades. The blades of the Polychlorophyllae were said to be flat and those of the Oligochlorophyllae generally involute. This division of the genus by Saint-Yves parallels the first pair of choices in the taxonomic keys of Merrill (1902 Hitchcock (1935), Swallen (1939), and Chase (1950), wherein "blades flat" or "blades involute" are used as contrasting criteria. Saint-Yves further subdivided the two groups into four species and a hybrid each, based upon features of the inflorescences. Four of the eight species he recognized, S. maritima, S. cynosuroides, S. juncea, and S. densiflora, represent combinations of a number of species of other authors, most of which were assigned by him to infraspecific ranks. The other four species, S. arundinacea, S. ciliata, S. gracilis, and S. foliosa, were not subdivided. Two hybrids, S. cynosuroides X gracilis and X S. longispica, were described. The hybrid origin of X S. longispica was briefly discussed.

In modern taxonomy, increasing attention is being paid to cytotaxonomic investigations. Important contributions to an understanding of cytology of the genus Spartina have been made by Huskins (1931) and Church (1936, 1940). Huskins confirmed the hypothesis of the hybrid origin of S. townsendii with cytological data. This work is reviewed more fully in connection with the discussion of S. townsendii.

Church (1940) investigated chromosome numbers in the North Ameri-

can species and reported the existence of a high degree of polyploidy with chromosomes present in multiples of seven. This, he concluded was evidence that seven is the basic number within the genus. Five of the nine species, S. bakeri, S. caespitosa, S. cynosuroides, S. gracilis, and S. spartinae, were found to have the hexaploid number of forty-two. These determinations were based upon a single specimen of each species. A single specimen of S. leiantha (S. foliosa) was found to have the octoploid number of fifty-six. The remaining three species, S. alterniflora, S. patens, and S. pectinata, were each shown to possess an intraspecific polyploid series. Within S. alterniflora, an octoploid and a decaloid were discovered which were observed to differ in habitat preference and morphology. Spartina patens was reported to consist of three different polyploids. Specimens from Massachusetts, Virginia, and Florida were shown to possess the tetraploid, hexaploid, and octoploid number of chromosomes, respectively. Spartina pectinata was observed to have both the hexaploid and dodecaploid number of chromosomes. New England specimens were hexaploid, while germinating seeds from Nebraska material were dodecaploid. No morphological comparisons were reported because the dodecaploids did not mature.

MATERIALS AND METHODS

The materials used in this study were largely dried and pressed specimens from a number of institutional herbaria in the western hemisphere together with the author's collections from stations within the United States. Because of the large number of specimens examined during the course of this investigation, citation of specimens has been omitted except in the cases of type specimens and certain rare instances. Where citation is made, each is followed by an appended key letter or letters which identify the institution. These key letters are the standardized abbreviations given by Lanjouw and Stafleu (1952) in Index Herbariorum. A complete list of herbarium specimens studied is on file in the herbarium of the Iowa State College.

Collections were made by the author during the months of July, August, and September, 1952, at selected coastwise stations ranging from Galveston, Texas eastward to Florida and northward to New Hampshire. Additional collections were made at localities in Michigan, Indiana, Wis consin and Iowa.

Herbarium specimens were prepared from field material. The plants were dried overnight in presses suspended over kerosene lanterns. Except under the most inclement weather conditions, most of the specimens were dry enough for storage within 48 hours. However, specimens of Spartina alterniflora with their thick, fleshy, succulent culms required some additional care, often having to be left in the presses for a week or more.

Preliminary investigation had shown that some features of the inflorescences of species of Spartina possessed much measurable variability. In order to survey more adequately the ranges in variability, numerous panicles were collected and stored in small paper sacks. This procedure was followed for two reasons; first, to accumulate quantities of material

from large, pure stands in order that an adequate sampling of variability be secured, and second, to utilize a rapid and easy method of collecting small amounts of material from as many stations as possible throughout the area visited. Where the plants were found in large, dense stands, a reasonable attempt was made to get as representative a sample as possible. The plants often tend to grow in small clumps with several culms arising from the same rhizome. In no case was more than one panicle per clump selected.

In order to obtain material for cytological study of chromosome numbers, fresh root tips were killed and fixed in the field in freshly mixed Carnoy's fluid consisting of one part glacial acetic acid and two parts absolute alcohol. Only specimens to which the root tips were physically connected became a part of that particular collection. The voucher specimens from which the root tips were taken were deposited in the herbarium of Iowa State College.

Study of specimens consisted largely of measurement of various parts of the plants and critical examination of certain features not amenable to measurement. The general procedure used in dealing with all species is presented below. Occasionally, measurement or examination of a specific character was found to have some value only for a problem concerned with a single species. Methods involved in cases of this sort are described in the text. Measurement of anther lengths and morphological parts requiring accuracy to 0.1 mm were made with the aid of a Spencer low-power binocular microscope equipped with 1X, 2X, and 3X objectives and 10X field oculars. The right ocular was furnished with an ocular micrometer that had been calibrated with a stage micrometer. All other measurements were made with an ordinary 15 cm rule graduated in millimeters. Measurement data are reported in metric units.

Culm height was measured from the base of the culm to the apex of the panicle. Non-flowering culms were omitted from the study.

Measurements of leaf blade lengths and widths were made on the second blade from the summit. Certain exceptions to this procedure are noted in the text. Blade width measurements were made at a point approximately 1 cm from the base of the blade because the tissue at the base was often flanged out, cracked or broken. In the case of tightly involute blades, the tissue was softened with a detergent-methyl alcohol solution (Pohl, 1954), and flattened for more accurate determination of width.

Measurement of the ligule was made on the second leaf from the summit. In the event that lengths of the hairs varied, as they frequently did, an estimated average was struck.

Panicle length was measured from the point of insertion of the lowest spike to the tip of the terminal spike or to the tip of the panicle axis if it exceeded the spike. Only panicles with normally tightly appressed spikes appear to have a measurable width. The width of those panicles with somewhat spreading spikes seems to be influenced by degree of maturity and certainly by the pressing and mounting operations. Where width of the panicle was ascertainable, measurement was made at a point midway between base and apex.

Measurement of spikes was made from the point of insertion on the panicle axis to the tip of the terminal spikelet or to the tip of the spike

rachis if it exceeded the spikelet. Spike length was measured on a median or near median spike. Exceptions to this procedure are noted in the text. In the event that two-spiked panicles were encountered, the basal spike was measured. Occasionally the length of the peduncle proved useful. Its length was measured along the spike rachis from the point of insertion on the panicle axis to the base of the lowest spikelet.

Length of the spikelet was found to be coincident with the length of the second glume except rarely, where the floret exceeded the second glume. In such cases, spikelet length was measured to the tip of the floret. Spikelets are usually sessile but occasionally some are pedicellate. The spikelet length value in these instances included the pedicel.

The degree of crowding of spikelets along the rachis of a spike has been shown to have some taxonomic significance. A fairly satisfactory numerical expression of the crowding was derived by dividing spikelet number into spike length. This numerical equivalent seems to achieve greater precision than do the words imbricate, crowded, remote, and similar terms. However, the numerical values are not without some minor inaccuracies, for no attention was given to spikelet or peduncle lengths or variations in the lengths of distances between spikelets.

Attempts were made to determine chromosome numbers for some of the species. A smear technique was used throughout the investigation. The hand and camera lucida drawings of the chromosomes have been filed with the voucher specimens.

The data supporting taxonomic conclusions are presented in the form of descriptions, tables, histograms, maps, illustrations, and scatter diagrams. In compiling distributional data for presentation on maps, only specimens which had actually been seen and verified by the author were included. The drawings of spikelets were made with the aid of a camera lucida attached to the Spencer binocular microscope described above. Unless otherwise indicated, the drawings were originally 10X or 20X and were reduced to 3.75X or 7.5X for presentation in this paper.

Liberal use has been made of the scatter diagram allowing for the simultaneous presentation of two variables. The methods of Anderson (1949) have been followed in the construction of these diagrams. In general, the purpose in using the scatter diagram was to show whether a population sample was homogeneous or actually divisible in regard to the two variable characters utilized. In some few cases, ratios rather than absolute measurements were introduced into the diagrams.

In the systematic treatment which follows, the taxa recognized in this paper are discussed in considerable detail. Complete synonomies are given and, where nomenclatural problems warrant, evidence is presented showing why the names are regarded as synonyms. Descriptions are offered and are partially supported by illustrations of spikelets.

A discussion of the important taxonomic distinctions between the taxa is deferred to the section of this paper dealing with keys to the species.

TAXONOMIC CONSIDERATIONS

The Genus Spartina

Spartina Schreb. Gen. Pl. ed. 8. 43 (1789)
Trachynotia Michx. Fl. Bor. Amer. 1:63. (1803)
Limnetis Rich. in Pers. Syn. Pl. 1:72. (1807)
Ponceletia Thouars, Fl. Trist. Acugn. 36. (1811)
Tristania Poir. in Lam. Encycl. Suppl. IV. 526. in obs. (1816)
Solenachne Steud. Syn. Pl. Glum. 12. (1855)
Chauvinia Steud. Syn. Pl. Glum. 362. (1855)

Description

Plants perennial; culms 0.1--3.5 meters tall, erect, terete, caespitose from knotty bases or solitary from strong, scaly rhizomes; cauline leaves 3--15; sheaths firm, smooth to somewhat striate; ligule a ring of hairs; blades flat or involute; panicle 3--70 cm long; panicle axis usually 3-angled; spikes 1--75; appressed or spreading, alternately to irregularly arranged along a common axis; rachis of the spikes 3-angled; spikelets 1-flowered, laterally compressed, usually sessile in two rows on two sides of the 3-angled rachis, articulating below the glumes; first glume shorter than the floret, 1-nerved, the keel glabrous, pilose or hispid; second glume usually longer than the floret, 1--3-nerved, the keel glabrous, pilose or hispid; lemma shorter than the palea, usually firm in texture, 1--3-nerved, the lateral nerves obscure, the keel glabrous, pilose or hispid; palea thin and papery, 2-nerved, obscurely keeled, the keel glabrous or rarely hispid near the tip; stamens 3; ovary 1, stigmas 2, plumose; lodicules 0; seeds not commonly produced, plants apparently reproducing mostly by vegatative means; basic chromosome number 7.

Discussion

Spartina schreberi Gmel. has been regarded as the type species of the genus but unfortunately, the name has never enjoyed nomenclatural standing. Gmelin (1791) supplied the specific epithet but failed to provide a description, a plate or a reference to an earlier description, the name was not validly published. If a specimen upon which the name is based ever existed, its whereabouts at the present time is unknown. The invalid binomial, Spartina schreberi, is the only one, to the author's knowledge, that has ever been cited as the name of the type species. If the genus Spartina is to be properly typified, it appears necessary that another species be chosen as the type. Accordingly, the well-known and widely distributed Spartina cynosuroides (L.) Roth is designated the type species. The holotype is conserved in the herbarium of the British Museum.

Spartina, a genus of grasses, has been placed in the tribe Chlorideae, a heterogeneous assemblage of genera held together solely by the presence of a one-sided arrengement of spikelets in spikes. In this genus, the spikes appear to be one-sided although the spikelets are actually arranged in two rows on two sides of a somewhat flattened, triangular

rachis. In no other particulars of the inflorescence, except in the character linking all members of the subfamily *Festucoideae* does *Spartina* agree with the other genera referred to the *Chlorideae*. In the absence of more precise data concerning phylogenetic relationships, it seems advisable for the present to consider the genus a member of the *Chlorideae*.

Within the genus, three complexes of species may be delineated. Each of the complexes lends itself quite well to treatment as a subgenus, but owing to the small number of species, naming of subgeneric taxa does not seem advisable. The three complexes with their included species are presented in Table 1.

Table 1. Three Complexes of the Genus *Spartina* with Included Species.

Complex 1	Complex 2	Complex 3
Spartina arundinacea	*Spartina alterniflora*	*Spartina bakeri*
S. ciliata	*S. foliosa*	*S. X caespitosa*
S. spartinae	*S. longispica*	*S. cynosuroides*
	S. maritima	*S. densiflora*
	S. neyrautii	*S. gracilis*
	S. townsendii	*S. patens*
		S. pectinata

The first of the three complexes consists of those species with numerous short, closely imbricate spikes, so arranged that the entire panicle has a smooth, cylindrical contour. The culms are hard and slender. The spikelets are always pubescent, at least on the keels of the glumes, and the pubescence is strongly hispid or villous. While rhizomes may be produced, they are seldom longer than a few centimeters at most.

The second complex contains those species characterized by more or less thick, fleshy, succulent culms; smooth, glabrous leaves; and spikelets that are usually less closely imbricate than those of the species within the other complexes. The plants rarely show a tendency to be streaked or tinged with purple, though they may often become somewhat brown in color. A distinctly disagreeable odor emanating from the fresh culms may persist in dried specimens for several months or more.

Plants of the third complex are characterized by hard culms; scabrous leaves (at least on the margins); more or less spreading spikes; and usually closely imbricate spikelets. The inflorescence rarely assumes a smooth, cylindrical contour. Pubescence on the keels of glumes and lemmas is hispid. Very often plants of this complex are streaked or tinged with purple, especially in the inflorescnnces and occasionally on the sheaths and culms.

SYNOPSIS OF THE SPECIES

The sixteen species of the genus Spartina are treated below in synoptic form. In addition to this synopsis, keys to the species are provided in a succeeding section.

1. Panicle spikelike, smoothly cylindric; spikes numerous, short, appressed, often twisted; culms slender, hard, not fleshy nor succulent; rhizomes short or wanting; keels of the glumes hispid or villous. 2

1. Panicle not commonly spikelike (except in S. foliosa); spikes appressed or spreading; culms thick, fleshy, succulent, having a disagreeably sulphurous odor when fresh; rhizomes usually flaccid, scales inflated; pubescence on the spikelets usually pilose; plants rarely streaked or tinged with purple (observed only in a single specimen of S. foliosa). 3

1. Panicle not spikelike; spikes usually spreading; culms hard, not fleshy nor succulent; rhizomes when present firm, scales not inflated; pubescence on the spikelets hispid to pectinate; plants often streaked or tinged with purple. 6

2. Spikelets lanceolate, exceeding 8 mm in length; plants of the islands of Tristan de Cunha, Diego Alvarez, and St. Paul and Amsterdam. . . . . 1. Spartina arundinacea

2. Spikelets ovate, densely pilose, exceeding 8 mm in length; plants of the sandy beaches and dunes of southern Brazil, Uruguay and northern Argentina. . . . . 2. Spartina ciliata

2. Spikelets lanceolate, not usually exceeding 8 mm in length; plants distributed from Florida to Costa Rica along the Gulf of Mexico and Caribbean Sea and in south-central Paraguay and northern Argentina. . . . . 3. Spartina spartinae

3. Spikes usually short, closely appressed, crowded near the apex of the panicle, often twisted; spikelets glabrous to pilose; glumes usually curved; plants of California and Baja California. . . . . 5. Spartina foliosa

3. Spikes elongate, not usually closely appressed; not noticeably crowded near the apex of the panicle, never twisted; spikelets glabrous to pilose; glumes not curved; plants distributed elsewhere. 4

4. Spike rachis exceeding 1 mm in width; spikelets usually appressed, moderately imbricate, not copiously pilose; plants of the River Plate region of Argentina and Uruguay. . . . . 6. Spartina longispica

4. Spike rachis not usually exceeding 1 mm in width; spikelets not usually appressed, remotely to closely imbricate, not copiously pilose; plants of coastal marshes of North America, South America and Europe. . . . . 4. Spartina alterniflora

4. Spike rachis more or less than 1 mm in width; spikelets usually copiously pilose, appressed or spreading, moderately imbricate; plants of Europe and Africa. 5

5. Blades exceeding 17 cm in length, not readily disarticulating from the sheath; spike rachis exceeding 1 mm in width; spikelets appressed; plants of southwestern France. . 8. Spartina neyrautii

5. Blades not exceeding 12 cm in length, readily disarticulating from the sheath; spike rachis not usually exceeding 1 mm in width; spikelets appressed or spreading, not exceeding 15 mm in length; plants of the coastal marshes of western Europe and Africa. 7. Spartina maritima

5. Blades exceeding 12 cm in length, not usually disarticulating from the sheath; spike rachis usually exceeding 1 mm in width; spikelets usually spreading, exceeding 15 mm in length, plants of the coastal marshes of western Europe. . . 9. Spartina townsendii

6. Rhizomes wanting or short and at once upturned; culms caespitose; extra-vaginal shoots closely appressed to the culm; spikes usually fewer than 15. 7

6. Rhizomes present; culms usually solitary; spikes few to many. 8

7. Second glume 1-nerved, tip usually acute, culms not exceeding 1.5 meters in height; plants of Brazil, Uruguay, Argentina, and Chile. . . . . 13. Spartina densiflora

7. Second glume 2--3-nerved, tip obtuse to acuminate, culms usually exceeding 1.5 meters in height; plants of salt or fresh water habitats in Florida and Georgia. . . . . . 14. Spartina bakeri

7. Second glume 3-nerved, tip acuminate to aristate; culms not exceeding 1.3 meters in height; plants of disturbed ground in and around coastal marshes from Maine to Maryland. . . . . 11. Spartina X caespitosa

8. Rhizomes thick and hard, light brown to brownish-purple, scales closely imbricate; blades usually flat; spikes few to many. 9

8. Rhizomes thin and wiry, whitish, scales not closely imbricate; blades usually involute; spikes fewer than 15. 10

9. Second glume not awned; first glume usually shorter than one-half the length of the second; lemma not deeply bilobed at the

tip, tip acute to obtuse; plants of the eastern seaboard from Massachusetts to Florida and along the coast of the Gulf of Mexico from Florida to Texas. . . . 12. Spartina cynosuroides

9. Second glume aristate to awned; first glume usually longer than one-half the length of the second; lemma deeply bilobed, tip acuminate. 10

10. Culms usually exceeding 1.2 meters in height; spikes commonly more than 10; second glume usually long-awned; plants of Nova Scotia and New Brunswick west to Alberta, south to Virginia, Kentucky, Texas, and Washington. . . . . 16. Spartina pectinata

10. Culms not usually exceeding 1.2 meters in height; spikes fewer than 10; second glume acuminate to aristate; plants of disturbed ground in and around coastal marshes from Maine to Maryland. . . . . 11. Spartina X caespitosa

11. Spikes slender, not usually plosely appressed to the panicle axis; pubescence on keels of glumes and lemmas hispid; plants of eastern North America along the Atlantic seaboard from Nova Scotia to Florida, inland in Michigan and New York, Gulf and Caribbean coasts from Florida to Honduras, throughout the West Indies, and in Europe in the western Mediterranean basin. . . . . 15. Spartina patens

11. Spikes short, broad, closely appressed to the culms; pubescence on keels of glumes and lemmas copiously long-hispid; plants of plains and mountain regions of North America from Mexico to the Mackenzie Territory. . . . . 14. Spartina gracilis

1. SPARTINA ARUNDINACEA

Spartina arundinacea (Thouars) Carmich. Trans. Linn. Soc. 12:504. (1819)
Ponceletia arundinacea Thouars, Fl. Trist. Acugn. 36. (1811) (Type in P from Tristan de Cunha)
Tristania arundinacea (Thouars) Poir. in Lam. Encycl. Suppl. IV:526. (1816) in obs.

Description (Plate 1, a-c)

Culms to 1.5 meters tall, erect, terete, indurate, striate, glabrous, from knotty bases; rhizomes short, thick, upturned; sheaths indurate, often shining, smooth to somewhat striate, margin of the orifice pilose; ligule a ring of hairs about 1 mm in length; blades involute, glabrous to scabrous on the adaxial surface, glabrous on the abaxial, scabrous on the margins, tip acuminate, the terminal blade not exceeding the panicle; panicle up to 16 cm long, 1--2 cm wide; panicle axis 3-angled, glabrous

to sparingly hispid on the angles, spikes up to 50, 2--4 cm long, 2--5 mm wide, flattened dorsiventrally, irregularly arranged, tightly appressed, closely imbricate, twisted, giving the panicle a smooth contour; rachis of the spikes glabrous to sparingly hispid on the angles not prolonged beyond the terminal spikelet; spikelets 20--40, 6--12 mm long, 1--3 mm wide, alternate, tightly appressed, closely imbricate, often pedicellate, the pedicel about 1 mm long; first glume linear, 4--10 mm long, glabrous, keel hispid, tip acuminate; second glume 6--12 mm long, glabrous to minutely hispidulous, keel hispid above, margins glabrous to hispidulous, tip acuminate; lemma glabrous to minutely hispidulous, keel hispid above, often glabrous below, margins glabrous, tip obtuse, shallowly lobed; palea thin and papery, margins notched at the apex of each nerve, tip obtuse or rounded, slightly exceeding the lemma; anthers rarely exceeding 3 mm in length; stigmas usually subequal.

Observations

As only four specimens of this species were available for examination, it is impossible to show ranges in the variability of morphological features. The descriptive material above was taken from the specimens examined. Admittedly, these constitute a rather unsatisfactory sample, all the more so because of the scattered distribution of the species. Chromosome numbers are unknown for this species.

Nomenclature

The earliest description of the plant is that of Du Petit-Thouars (1811) under the genus Ponceletia. Although the type specimen was not seen, study of the detailed description shows that Spartina arundinacea is properly typified. The combination S. arundinacea Carmich. has been used by other authors, but inasmuch as the name-bringing synonym was cited in synonomy by Carmichael (1819) it appears that the author citation should include the original authority for the epithet.

Distribution

Of the four specimens examined, two were from the island of Tristan de Cunha (37°06' S., 12°17' W.) and another from the islands of St. Paul and Amsterdam (38°43' S., 77°32' E.). The fourth is merely labeled St. Paul Island near Tristan de Cunha. This specimen, from the Torrey Herbarium (NY), was in all probability collected on St. Paul Island. No apparent morphological differences exist between specimens from the two widely separated island groups.

Hemsley (1844) reports the plant to be common on all three of the islands which make up the Tristan de Cunha group as well as on the two islands, St. Paul and Amsterdam. Christopherson (1934) found the plant occurring abundantly on Gough Island (Diego Alvarez) 220 miles southeast of Tristan de Cunha.

Little precise data are available concerning the habitat of the species. Carmichael (1819) states that the plants grow abundantly in thick clumps at the base of the volcanic mountain on Tristan de Cunha. The species has been observed to flower in February.

Specimens examined. St. Paul and Amsterdam, Nauman 112 US; St. Paul near Tristan de Cunha, NY; Tristan de Cunha, MacGillivray 345 GH; Stableford ISC.

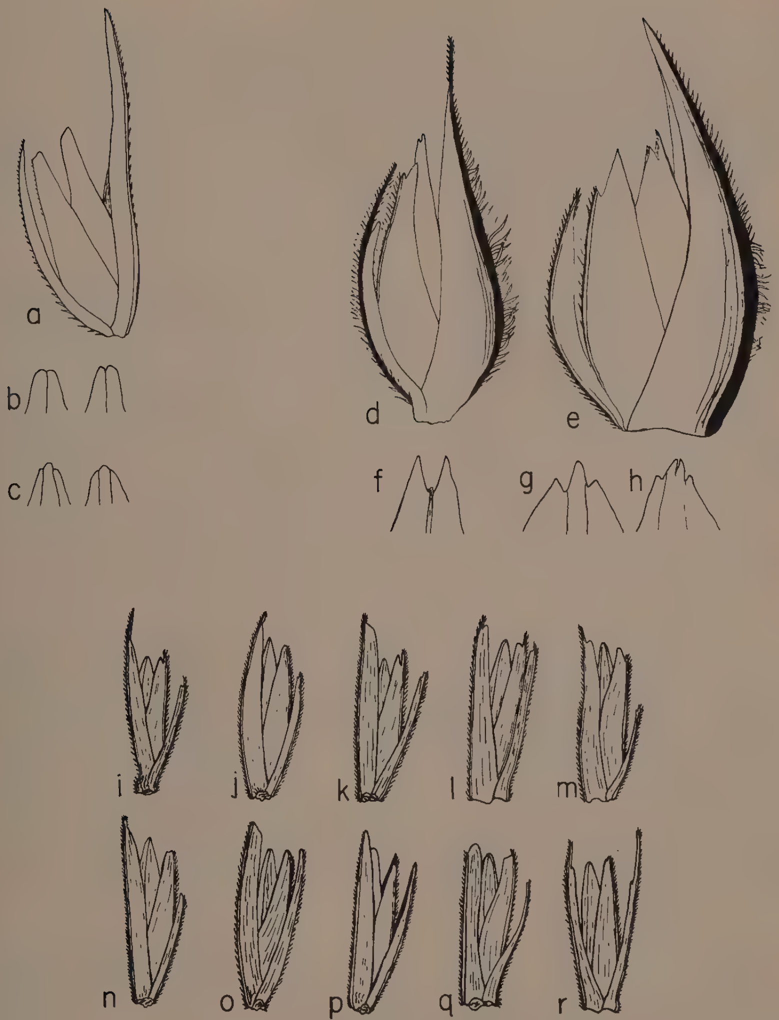

PLATE I

a-c. Spartina arundinacea. a. spikelet 3.75X, b. lemma tips 7.5X, c. palea tips 7.5X.

d-h. Spartina ciliata. d-e. spikelets 3.75X, f. lemma tip 7.5X. g-h. palea tips 7.5X.

i-r. Spartina spartinae. i-r. variations in spikelets 3.75X.

2. SPARTINA CILIATA

Spartina ciliata Brong. Du Perr. Voy. Coq. Bot. 15. (1829) (Type in P from Isle of St. Catherine, Brazil)
Spartina ciliata Kunth. Rev. Gram. 1:94. (1829) *nomen nudum*.
Spartina coarctata Trin. Mem. Acad. St. Petrsbg. Sci. Nat. VI. 6:110. (1836) (Type in LE from Uruguay)
Solenachne phalaroides Steud. Syn. Pl. Glum. 12. (1855) (Type in P from Isle of St. Catherine, Brazil)

Description (Plate 1, d-h)

Culms to 2 meters tall, erect, indurate, terete, glabrous, caespitose from hard, knotty bases, occasionally with short rhizomes; sterile leaf-bearing shoots often arising from the lower nodes, these tightly appressed to the culm; sheaths smooth, glaucous or shining, the lower much broken by the emergent shoots, margin glabrous, hyaline, margin of the orifice densely pilose; ligule a ring of hairs 2--3 mm long; blades narrowly involute, scabrous on the adaxial surface, glabrous on the abaxial, glabrous to scabrous on the margins, tip acuminate; panicle 15--40 cm long, 1--2 cm wide; panicle axis 3--4-angled, twisted, sparingly pilose; spikes 10--50, 2--5 cm long, flattened dorsiventrally, irregularly arranged, tightly appressed, densely imbricate, twisted giving the panicle a smooth contour; rachis of the spikes pilose on the angles, not prolonged beyond the terminal spikelet; spikelets 15--25, 10--20 mm long, 4--8 mm wide, alternate, tightly appressed, closely imbricate, often twisted; first glume linear, 6--10 mm long, thin and papery, glabrous to sparingly pilose, keel pilose below, becoming strongly hispid above, margins often hispidulous; second glume 12--20 mm long, thin and chaffy, glabrous to sparingly pilose, keel broad and thick, densely pilose below, becoming strongly hispid above, tapering into a short, sharp-pointed awn, margins hispidulous; lemma glabrous, the upper two-thirds of the keel pilose, margins hispidulous, produced beyond the keel forming a sharply bifid apex; palea thin and membranaceous, margins notched at the apex of each nerve, tip obtuse or rounded, slightly exceeding the lemma; anthers 4--7 mm long, often purple.

Observations

Specimens of *Spartina ciliata* are essentially uniform throughout the geographic range, although some variation does occur in height of the culm and length of the panicle. These differences are, in all probability, due to environmental circumstances. None of the variations could be correlated with geographic distribution. Chromosome numbers in this species are unknown.

Nomenclature

The binomial *Spartina ciliata* has been attributed to both Brongniart (1829) and Kunth (1829). The valid name is Brongniart's, as Kunth's was not accompanied by a description until a later publication (Kunth, 1833). The type specimen was not seen but a fragment deposited in the U.S. National Herbarium was available for study.

Distribution

The species is limited to the east coast of South America, ranging from south-central Brazil to Argentina.

It grows in dense clumps on sandy beaches and dunes well above the intertidal zone. Parodi (1919) included a photograph showing the typical habitat on the sandy coastal areas. The species flowers from November to May.

3. SPARTINA SPARTINAE

Spartina spartinae (Trin.) Hitchc. Contr. U.S. Nat. Herb. 17:329. (1913)

Vilfa spartinae Trin. Mem. Acad. St. Petrsbg. Sci. Nat. VI. 6:82. (1840) (Type in LE from Texas)

Spartina junciformis Eng. and Gray. Bost. Jour. Nat. Hist. 5:238. (1847) (Type in GH from Texas)

Spartina gracilis Hook. ex Chap. Fl. So. U.S. ed.1. 556. (1860) non Trin. (1840)

Spartina gouini Fourn. Mex. Pl. 2:135 (1886) (Type in P from Mexico)

Spartina multiflora Vasey ex Beal, Grasses No. Amer. 2:400 (1896) pro syn. (Type in US from Florida)

Spartina pittieri Hack. Oesterr. Bot. Ztschr. 52:237. (1902) (Type in W from Costa Rica)

Spartina densiflora var. obtusa Hack. Fedde Rep. Nov. Spec. 6:345. (1909) (Type in W from Paraguay)

Spartina argentinensis Par. Rev. Fac. Agron. Vet. Buenos Aires 2:258. (1919) (Type from Argentina)

Spartina densiflora Brong. var. junciformis (Eng. and Gray) St.Y. Cand. 5:77. (1932) (Based on S. junciformis Eng. and Gray)

Spartina densiflora Brong. var. junciformis (Eng. and Gray) St.Y. subv. argentinensis (Par.) St.Y. Cand. 5:79. (1932) (Based on S. argentinensis Par.)

Spartina densiflora Brong. var. junciformis (Eng. and Gray) St.Y. subv. genuina St.Y. Cand. 5:78. (1932) (Based on S. junciformis Eng. and Gray)

Spartina densiflora Brong. auct. non Beal, W.J. Grasses No. Amer. 2:396. (1896)

Description (Plate 1, i-r)

Culms to 2 meters tall, erect, terete, indurate, commonly glabrous, occasionally glaucous, from hard, knotty bases, rhizomes wanting; nodes often exposed; sheaths short, glabrous, occasionally glaucous, sparingly scabrous on the margins, margin of the orifice glabrous to hispid, never pilose; ligule a ring of hairs 1--2 mm long; blades involute when fresh, up to 5 mm wide, scabrous on the adaxial surface, glabrous on the abaxial, scabrous on the margins, tip acuminate; panicle 6--70 cm long, 4--20 mm wide; panicle axis 3--4-angled, often scabrous on the margins, twisted; spikes 6--75, 0.5--7 cm long, the lower often the longer, 2--4 mm wide, alternately to irregularly arranged, tightly appressed, closely imbricate, flattened dorsiventrally; rachis of the spikes glabrous to scabrous on the angles; spikelets 10--60, 4--8(-10) mm long, the lower

often the longer; first glume linear, 2--6(-8) mm long, glabrous to hispidulous, keel hispid, tip acuminate; second glume 4--8(-10) mm long, glabrous to hispidulous, keel hispid, tip acuminate to obtuse; lemma glabrous to hispidulous, upper two-thirds of the keel hispid, tip usually acuminate, rarely obtuse; palea thin and papery, often minutely hispid near the tip, tip acuminate to obtuse; anthers 3--5 mm long, occasionally purple; somatic chromosome numbers 28, 42.

Observations

Certain vegetative characters of Spartina spartinae show measurable variability. Data were obtained from specimens from across the entire range of geographic distribution of the species (Table 2). Mean and extreme values for height of the culm, length of the blade of the second leaf from the apex and width of the blade were recorded by geographic areas. Plants of the Yucatan Peninsula are included with those from Central America and Mississippi specimens are included with those of Texas and Louisiana.

Table 2. Morphological Characters of S. spartinae Based on Observations of 119 Specimens.

		Height of culm (cm)	Blade length (cm)	Blade width (mm)	Panicle length (cm)	Spike length (cm)
Florida	extreme	38.0	26.0	2.0	7.0	1.0
	mean	89.5	33.3	2.6	17.0	2.3
	extreme	184.0	54.0	3.5	45.0	3.4
Texas	extreme	49.0	21.0	1.5	8.0	1.1
and	mean	93.8	37.1	2.8	17.3	2.3
Louisiana	extreme	200.0	58.0	4.1	38.0	3.5
Mexico	extreme	46.0	12.0	1.5	8.0	1.5
	mean	104.3	28.2	3.0	20.1	2.4
	extreme	140.0	44.0	4.5	35.0	3.6
Central	extreme	120.0	42.0	2.9	20.0	1.4
America	mean	161.1	82.7	3.4	42.1	2.8
	extreme	195.0	125.0	4.5	61.0	4.5
South	extreme	78.0	22.0	1.5	14.5	2.0
America	mean	119.4	32.6	3.0	25.6	2.9
	extreme	166.0	51.0	4.0	39.0	4.2
Total	extreme	38.0	12.0	1.5	7.0	1.0
	mean	105.7	39.7	2.9	21.6	2.4
	extreme	200.0	125.0	4.0	61.0	4.5

The mean value for culm height in the Central American collections is considerably higher than the mean value for the total population. Because the measurement data from these Central American collections were taken largely from specimens collected near Belize, British Honduras, it may be that the results do not accurately show the variability within the Central American segment of the population. Corroborative evidence supporting this assumption is provided by Swallen (1932) who states that specimens of S. spartinae from the Mexican portion of the Yucatan Peninsula do not exceed 150 cm in height. Although taller plants are apparently more common in parts of Central America, there is, in the author's collections from Cameron Parish, La., a specimen which is just 200 cm tall (Mobberley 59, ISC).

As in the case of the culm, the mean value of blade length in the Central American segment is much higher than that in other segments. However, the mean blade width value from this segment does not vary a great deal from the mean value for the total population sample.

Beal (1896) used the presence of exposed nodes as a vegetative character of taxonomic significance. Although this feature was observed in many of the specimens examined, its occurrence was not consistent enough in any one segment to warrant attaching any diagnostic value to it.

The general aspect of the panicle seems to show some uniformity throughout the population. The spikes are usually densely imbricate and flattened dorsiventrally. The entire panicle is given a smooth contour by the twisting of these flattened spikes. Occasionally the panicles become dense and heavy enough to nod. Some variation was observed in the lengths of panicles and spikes (Table 2). Higher mean values for panicle and spike length appear in the Central American material, but for the reason discussed above in connection with culm height these higher values are not thought to be significant.

Considerable variation was observed in the morphology of the spikelet, notably at the tip of the second glume. Plate 1, i--r, illustrates the range of variation which was encountered. The illustrations are not intended to portray all the existing variations, but are drawn from selected spikelets which are more or less representative of the entire population. An effort was made to learn whether the variability in the character of the tip is correlated with geographic distribution, but the various types were not limited to one particular geographic area, clone or panicle. However, some uniformity was found within individual spikes.

Relative lengths of first and second glumes have been found to be of diagnostic value in certain of the Gramineae. Appraisal of this feature in S. spartinae revealed that the second glume is about 2 mm longer than the first. In rare cases, spikelets were found in which the length of the first glume barely equalled one-half the length of the second; in one instance (Plate 1, r) the first glume exceeded the second in length.

The anthers show no particular features of diagnostic value. Occasionally purple anthers are found, but the majority are yellowish.

Among other morphological features which possess some taxonomic usefulness are the absence of rhizomes, the caespitose habit, numerous and closely imbricate spikes, length of the spikelets and pubescence on the spikelets. These features will be discussed in greater detail in another section of this paper dealing with the distinctions between species.

Chromosome numbers for S. spartinae have been reported from only one previous source (Church, 1940). His determination of the hexaploid number of 42 is not in agreement with this investigators findings in which the tetraploid number of 28 was discovered (Table 3). Church's report is based upon Florida material (Church 510, Miami, Fla.), while the author's determinations are bsed on Texas and Louisiana specimens.

Table 3. Chromosome Numbers in S. spartinae

Specimen		Chromosome number
Mobberley 26	Port Bolivar, Galveston Co., Texas	2n = 28
Mobberley 32	Sabine Pass, Jefferson Co., Texas	2n = 28
Mobberley 33	Sabine Pass, Jefferson Co., Tcxas	2n = 28
Mobberley 40	Sabine, Jefferson Co., Texas	2n = 28
Mobberley 41	Sabine, Jefferson Co., Texas	2n = 28
Mobberley 52	Hackberry, Cameron Parish, La.	2n = 28

Conditions found elsewhere in the genus indicate that polyploidy is more or less to be expected. Accordingly, Florida specimens were critically compared with specimens from Texas and Louisiana in an effort to learn whether the apparent cytologically differing segments of the population differed in any gross morphological features. No significant differences were uncovered in any of the traits compared.

Nomenclature

The name Spartina spartinae (Trin.) Merr. has been widely used despite its erroneous author citation. Merrill (1902) introduced the combination by transfer of Vilfa spartinae Trin., to Spartina but rejected it as meaningless. Hitchcock (1913) adopted the invalidly published combination and cited Merrill as the authority. There being no obstacle to the use of the combination, it may continue to be employed. However, under the provisions of Article 81 of the International Code of Botanical Nomenclature, the epithet is to be regarded as new under the authority of Hitchcock. The binomial with the proper author citation becomes Spartina spartinae (Trin.) Hitchc.[1]

A photograph of the type specimen of Vilfa spartinae was examined. This examination, coupled with a study of a fragment of the type (deposited in US), leaves no doubt as to the accuracy of the typification.

Spartina argentinensis was described by Parodi (1919). Although the type specimen was not available for examination, nothing appears in the description that would indicate that it is different from S. spartinae. Spikelet lengths are given as 5--7 mm, spikes 20--40 in number and

[1]The author is indebted to Dr. H.W. Rickett, bibliographer to the New York Botanical Garden, for assistance in the solution of this nomenclatural problem.

2--3 cm in length, but these values are met throughout the geographic range of S. spartinae. As may be seen from Parodi's published photograph of the type specimen (Parodi, 1919), the spikes seem somewhat less tightly appressed, However, several specimens with spikes tightly appressed, identified by Parodi as S. argentinensis, are deposited in the U.S. National Herbarium. It is apparent that Parodi did not regard this more or less lax attitude of the spikes as of fundamental taxonomic significance. In addition, this feature was observed occasionally among specimens from Texas and Mexico. Because nothing except geographic discontinuity allows a separation of the South American from the North American plants, it seems advisable to regard S. argentinensis as a synonym of S. spartinae.

Saint-Yves (1932) reduced S. spartinae to S. densiflora var. junciformis and erected within that variety two subvarieties, genuina and argentinensis, differentiated on the basis of geographic distribution, panicle length and length and appression of the spikes. The former subvariety is supposed to occur in North and Central America and have panicles 20--30 cm long and tightly appressed spikes 2--2.5 cm long. The latter subvariety is supposedly characterized by its occurrence in South America, panicles 30--35 cm long, and somewhat less tightly appressed spikes 3--4 cm long. This investigation has shown that S. spartinae (S. junciformis) is a species quite distinct from S. densiflora and that their combination by Saint-Yves is unwarranted. Effective separation of the two is discussed in another section of this paper dealing with distinctions between South American species of the genus. All available specimens of S. spartinae were evaluated in accordance with the criteria proposed by Saint-Yves in order to learn whether or not these subvarietal taxa may be distinguished from each other. Some of the South American specimens do have the spikes less tightly appressed but, as noted above in the discussion of S. argentinensis, the same condition was observed in North and Central American material. That the criteria concerning panicle and spike lengths are not answered is evident from the data presented in Table 2. Panicle and spike lengths of many North American specimens are in excess of the stipulated upper limits for the South American subvariety. Panicle lengths of many South American specimens are less than the stipulated lower limits for the North American subvariety. The least spike length value found among South American specimens is just equal to the stipulated lower limit for the North American subvariety. The foregoing evidence indicates that these subvarietal taxa have been erected without justification and, accordingly, they are treated as synonyms of S. spartinae.

Distribution

The distribution of Spartina spartinae is limited to the western hemisphere and consists of two disjunct geographic segments. In North and Central America the species ranges from Florida around the gulf coast to Texas, Mexico, and Costa Rica. A single specimen (Bailey 1011, US) is known from the Bahamas, B.W.I. Fig. 1 shows the distribution of the North and Central American segment of the population.

In South America, the species appears to have a more restricted distribution limited to Northern Argentina and Paraguay.

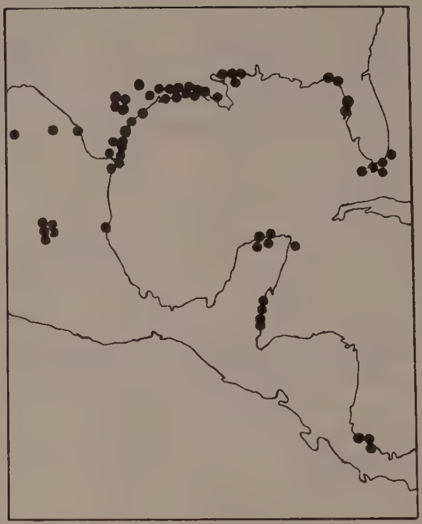

Fig. 1. Distribution of Spartina spartinae in North America

A condition which might bear further investigation is the inland distribution of the South American representatives. In South America, the species is apparently not known from the coastal areas. This is somewhat in contrast to the North and Central American situation where plants are found on the sandy beaches as well as some distance inland. Some Texas collections indicate that the plant may be found inland as much as 60 miles in the region of Gonzales County. Mexican collections show that the species occurs both coastwise and inland, often at considerable altitude. Comparison of the specimens from both areas shows no discrete morphological differences. The upland specimens tend to be a little less robust and often possess fewer spikes than do the coastal plants, but otherwise they are similar.

At collection stations in southeastern Texas and southern Louisiana, the author found the species to be very common. The plants grow in a variety of habitats from the sandy beaches, dunes, roadsides, roadside ditches and wet meadows to arid fields and pastures. In fields and pastures near the coast, the species is easily the most prominent if not the most abundant component of the vegetation. It has a rather striking appearance by virtue of the large, tall clumps (up to 70 cm in diameter) which seem to overtop the remainder of the vegetation. The clumps may have as many as forty or fifty fertile culms. Clumps on the beaches and dunes are usually somewhat smaller in diameter and less deeply rooted than those encountered in other habitats. Occasionally, clumps with only three or four fertile culms were found on the beaches.

The species does not seem to provide palatable forage; cattle were observed to turn it down in favor of the more succulent S. patens and species of Paspalum.

S. spartinae flowers from March to October in North America and from December to May in South America.

4. SPARTINA ALTERNIFLORA

Spartina alterniflora Lois Fl. Gall. 719. (1907) (Type from Bayonne, France)

Dactylis cynosuroides var. β L. Sp. Pl. ed.1. 1:71. (1753) (Type in BM from Virginia)

Dactylis maritima Walt. Fl. Car. 77. (1788) non Curtis (1787)

Trachynotia alterniflora (Lois.) DC. Fl. Fr. 6:279. (1815)

Spartina glabra Muhl. Descr. Gram. 55. (1817)

Limnetis glabra Nutt. Gen. 1:38. (1818) nomen nudum

Spartina laevigata Link, Jahr. Gewächsk. I. 3:92. (1820) (Type in B from North America)

Spartina brasiliensis Raddi, Agrost. Bras. Atti Del. Reale Accad. 2:21. (1823) (Type in PI from Rio de Janiero, Brazil)

Trachynotia alternifolia Steud. Nom. Bot. ed.2. 695. (1841) (Error for T. alterniflora)

Spartina dissitiflora Steud. Syn. Pl. Glum. 215. (1885) (Type in P from Bahia, Brazil)

Spartina stricta (Ait.) Roth var. alterniflora (Lois.) Gray, Man. Bot. ed.2. 552. (1856) (Based on S. alterniflora Lois.)

Spartina stricta (Ait.) Roth var. glabra (Muhl.) Gray, Man. Bot. ed.2. 552. (1886) (Based on S. glabra Muhl.)

Spartina stricta (Ait.) Roth var. maritima (Walt.) B.S.P. Prelim. Cat. N.Y. Pl.66. (1888) (Based on D. maritima Walt.)

Spartina glabra Muhl. var. alterniflora (Lois.) Merr. Bull. U.S. Dept. Agr. Pl. Ind. 9:9. (1902) (Based on S. alterniflora Lois.)

Spartina glabra Muhl. var. pilosa Merr. Bull. U.S. Dept. Agr. Pl. Ind. 9:9. (1902) (Type in US from Atlantic City, New Jersey)

Spartina alterniflora Lois. var. glabra (Muhl.) Fern. Rhod. 18:178. (1916) (Based on S. glabra Muhl.)

Spartina alterniflora Lois. var. pilosa (Merr.) Fern. Rhod. 18:179. (1916) (Based on S. glabra pilosa Merr.)

Spartina intermedia Bosc ex St.Y. Cand. 5:50. (1932) in obs.

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. Cand. 5:48. (1932)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. var. alterniflora (Merr.) St.Y. Cand. 5:53. (1932) (Based on S. alterniflora Lois.)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. var. alterniflora (Merr.) St.Y. forma gracilis St.Y. Cand. 5:54. (1932) (Type not designated)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. var. brasiliensis (Raddi) St.Y. Cand. 5:56. (1932)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. var. brasiliensis (Raddi) St.Y. subv. fallax St.Y. Cand. 5:57. (1932) (Type not designated)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. var. brasiliensis (Raddi) St.Y. subv. raddii St.Y. Cand. 5:56. (1932) (Based on S. brasiliensis Raddi)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St.Y. var. glabra (Gray) St.Y. Cand. 5:49. (1932)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St. Y. var. glabra (Gray) St. Y. subv. typica St. Y. Cand. 5:51. (1932) (Based on D. maritima Walt.)

Spartina maritima (Curt.) Fern. subsp. glabra (Muhl.) St. Y. var. glabra (Gray) St. Y. subv. pilosa (Merr.) St. Y. Cand. 5:51. (1932)

X Spartina merrillii Chev. Bull. Soc. Bot. Fr. 80:787. (1933) (Type in NY from Long Island, New York)

Description (Plate II, a-f)

Culms to 2.5 meters tall, erect, terete, fleshy, glabrous, usually solitary or in small clumps from widely spreading, elongate, flaccid, whitish rhizomes, scales inflated, not closely imbricate; sheaths smooth, the lower often wrinkled, glabrous, margin of the orifice glabrous to minutely pilose; ligule a ring of hairs 1--2 mm long; blades 3--25 mm wide, flat, occasionally becoming involute, glabrous to sparingly pilose on the adaxial surface, glabrous on the abaxial, margins usually glabrous, tip acuminate; panicle 10--40 cm long, often partially enclosed within the uppermost sheath; panicle axis 3-angled, glabrous, rarely sparingly scabrous on the angles; spikes 3--25, 5--15 cm long, alternate, loosely appressed, subremote to moderately imbricate, sessile or pedunculate; rachis of the spikes glabrous to sparingly scabrous on the angles, often prolonged beyond the terminal spikelet; spikelets 10--30, 8--14 mm long, alternate, spreading, occasionally appressed, subremote to closely imbricate; first glume linear, 4--10 mm long, usually longer than one-half the second, glabrous to sparingly pilose, keel glabrous to sparingly pilose, keel glabrous to sparingly pilose, margins glabrous, tip acute; second glume 8--14 mm long, glabrous to pilose, keel glabrous to pilose, tip acuminate to obtuse, occasionally apiculate; lemma glabrous to sparingly pilose, keel glabrous to very sparingly pilose, tip usually acuminate; palea thin and papery, slightly exceeding the lemma, tip obtuse or rounded; anthers 3--6 mm long; somatic chromosome numbers 56, 70.

Observations

Spartina alterniflora exhibits a high degree of variability in certain vegetative characters as well as in parts of the inflorescence. Among the characters analyzed were culm height, blade length and width, panicle length, spike number and length, spikelet number and length, ratio of spike length to spike number and pubescence on the spikelets. Of these characters, none could be correlated with another to show any population differences within the species.

The variability in culm height and spike number is less pronounced among specimens from the maritime provinces of Canada. These plants are smaller, less robust in appearance and have fewer spikes than some of the specimens from the remainder of the North American range of distribution. However, a number of specimens from the remainder of the range are quite similar to the more northerly specimens. Attempts to find suitable taxonomic distinctions between the more robust and less robust specimens failed.

Of all the characters examined, only two, the ratio of spike length to spikelet number and pubescence on the spikelets, exhibit variability that is definitely correlated with geographic distribution. Visual inspection

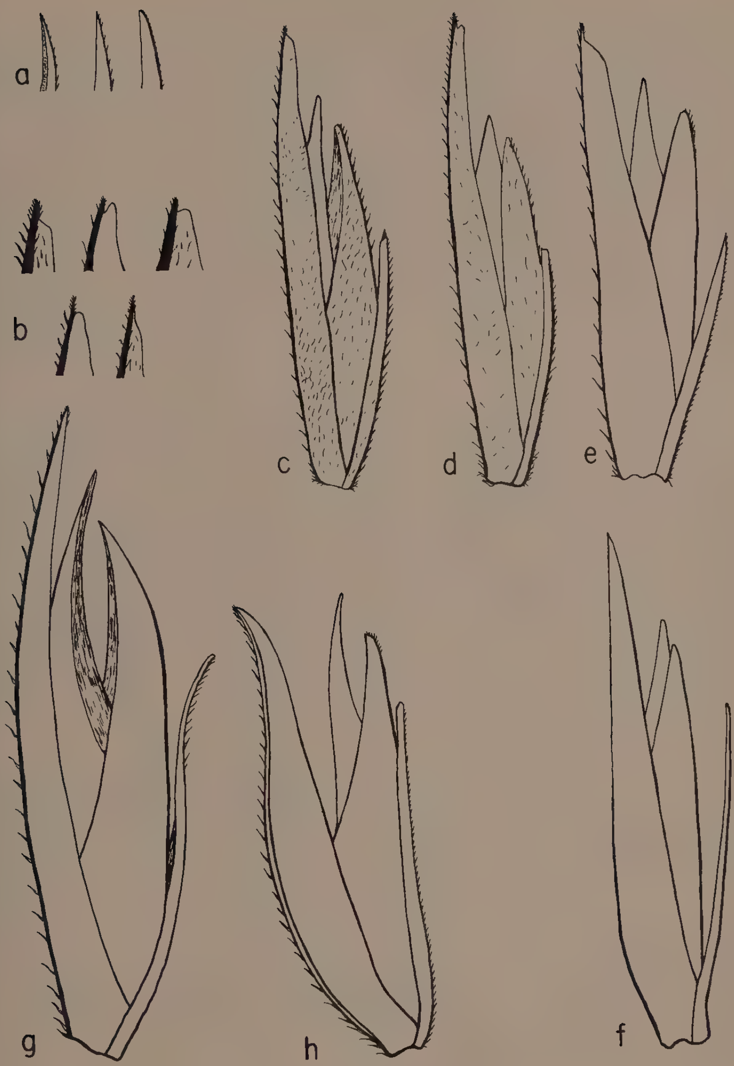

PLATE II

a-f. Spartina alterniflora. a. first glume tips 7.5X,
b. second glume tips 7.5X,
c-f. variations in spikelets and pubescence 3.75X.

g-h. Spartina foliosa. g-h. spikelets 3.75X.

of specimens collected from Maine northward to the maritime provinces of Canada showed that spikelets are not as closely imbricate along the spike as they are in plants from the remainder of the North American range. Further, plants from the southern half of the range (South Carolina to Texas) have spikelets that are noticeably less pubescent than those of plants from the northern half of the range. Plants of the intervening region (North Carolina to New Hampshire) seem to have spikelets more closely imbricate than do the northern specimens and considerably more pubescent than the southern specimens. In an effort to learn the extent of the variability exhibited by these two characters, the range of distribution of the species was divided into three segments on the basis of the observed variability. Section A included that part of the range from Maine northward, B from New Hampshire to North Carolina and C from South Carolina to Texas.

In order to effect a means by which numerous specimens could be compared, the two variables were reduced to numerical terms. A numerical equivalent for the degree of imbrication of spikelets is the quotient of spike length divided by spikelet number. Eight general classes of pubescence were recognized based upon the presence or absence of pubescence on laminae and keels of the second glume and lemma. In the interest of greater accuracy, the laminae were given independent consideration. While the amount of pubescence on any one part seems to vary somewhat (grading from glabrous to copiously pilose) a part was considered pubescent if it possessed at least five pilose hairs. Of all the combinations possible, only eight were found among the specimens examined. These varying degrees of pubescence were provided with numerical values according to the following table.

Table 4. Pubescence Values for Spartina alterniflora.

Second glume		Lemma		Numerical
Lamina	Keel	Lamina	Keel	value
Glabrous	Glabrous	Glabrous	Glabrous	1
Glabrous	Pilose	Glabrous	Glabrous	2
Glabrous	Pilose	Glabrous	Pilose	3
Glabrous	Pilose	Pilose	Glabrous	4
Pilose	Pilose	Glabrous	Glabrous	5
Pilose	Pilose	Glabrous	Pilose	6
Pilose	Pilose	Pilose	Glabrous	7
Pilose	Pilose	Pilose	Pilose	8

Three scatter diagrams (Fig. 2 A, B, C) are provided, one for each section of the range of distribution. Each specimen is introduced into the diagram by plotting its pubescence value against its numerical equivalent of imbrication of the spikelets. It may be seen from the diagrams that plants from the geographic extremes tend to group themselves into two somewhat segregated clusters. While the evidence presented shows population differences, the differences are not considered sufficient to

warrant the application of specific or infraspecific names. Some authors have sought to distinguish infraspecific taxa based upon the amount of pubescence on the lemma but it should be noted in this connection that pubescence on spikelets of some individual specimens varied from spikelet to spikelet. However, in this work, the pubescence value for any single specimen was always based upon the median spikelet of the median spike.

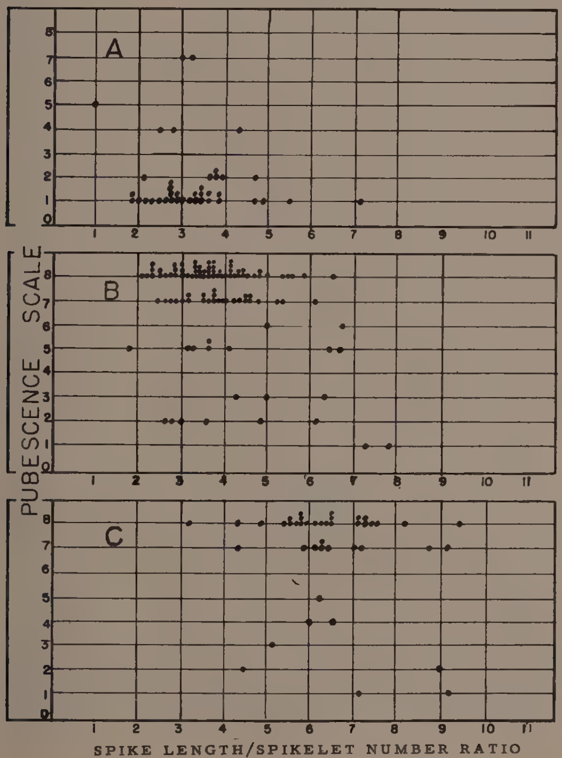

Fig. 2. Comparison of specimens of Spartina alterniflora of differing geographic localities by pubescence values and spikelet imbrication values.

A. Maine and the Maritime Provinces of Canada

B. New Hampshire to North Carolina

C. South Carolina to Texas

Church (1940) has shown the existence of two levels of polyploidy within this species; an octoploid (2n = 56) and a decaploid (2n = 70) which are supposedly morphologically and ecologically distinct. The octoploid form, found in the intertidal zone of the strand areas, was characterized by a height of 5--8 dm, leaf length of 2--4 dm, six to ten spikes and spikelets 10--12 mm long. The decaploid form, found along the muddy banks of tidal lagoons, was characterized by a height of 10--25 cm, leaf

length of 6--8 dm, fifteen to twenty spikes and spikelets 11--14 mm long. Nomenclaturally, the octoploid was referred to S. alterniflora var. glabra Fern. and the decaploid to S. alterniflora var. pilosa Fern. Some of the specimens from Section A of the range seem to agree with most of the criteria proposed and the less robust plants of this region may be the octoploid form. However, a majority of the specimens from Sections B and C of the range do not answer to the criteria. Many specimens with six to ten spikes exceed ten decimeters in height. In addition, many specimens with fifteen or more spikes have spikelets less than 11 mm in length. Two levels of polyploidy may exist throughout the range but, owing to the high degree of morphological variability, which is doubtless influenced by environmental conditions, they defy taxonomic separation.

S. alterniflora appears to be indigenous to the Americas but it has been introduced into other parts of the world, particularly England and France. The first record of a collection of this species in Europe is that of Loiseleur (1807), from the Bas-Pyrenees region of southwestern France. All specimens examined which had been collected from southwestern France agreed for the most part with the less robust North American form with its loosely imbricated spikelets. Although chromosome numbers are unknown for plants from France, it seems quite likely that this segment of the population may be the octoploid form. Specimens from collection stations in England and northern France exhibit about as much variability as those from the northern half of the North American range, although none of the European specimens are completely glabrous. Cytological studies have shown thé decaploid to be present in England (Huskins, 1931). The role of this decaploid in the formation of the allopolyploid S. townsendii is discussed more fully in connection with that species.

The range of the species also includes South America and the West Indies. The specimens from collection stations in South America do not exhibit characters by which they may be distinguished from North American material. They exhibit about the same range of variability with respect to the imbrication value (Figs 2, 6A). The pubescence on the lemma keel seems to be absent except for a few soft trichomes near the tip. This is a fairly constant feature of the South American material. A single character which may set apart many (but not all) of the South American specimens is the pedunculate spike. However, the presence of peduncles is not consistent; it is also occasional in North American material.

Nomenclature

Spartina alterniflora seems to be properly typified. Although the type specimen was not seen, study of the description verifies the accuracy of application of the name.

Numerous infraspecific taxa have been proposed but little credence can be given to the arguments supporting them. Fernald (1916, 1950) resolved a good share of the nomenclatural problems. His treatments correct many of the earlier names erroneously applied to the subdivisions of the species in eastern North America. According to Fernald, three "pronounced varieties" are to be found (Fernald, 1950), S. alterniflora Lois. "typical," S. alterniflora var. glabra (Muhl.) Fern. and S.

alterniflora var. *pilosa* (Merr.) Fern. The "typical" is supposedly distinguished from the two named varieties on the basis of the imbrication of the spikelets which are said to be subremote, barely overlapping. It is thought to be distinct from var. *glabra* in that lemmas are minutely pilose, and that the rachis of the spike is prolonged beyond the terminal spikelets. The "typical" is supposedly separable from var. *pilosa* solely on the basis of spikelet imbrication. Fig. 2, A, B, C, shows that there is no sharp line of demarcation separating two groups of the population upon this basis. Further, glabrous lemmas were observed in a number of the specimens with more remotely disposed spikelets. Exsertion of the rachis of a spike beyond the terminal spikelet is found quite consistently among specimens from all parts of the range of distribution. The fact that the rachis does not exceed the terminal spikelet in some specimens does not appear to be correlated with other morphological differences. No other criteria were found which would aid in the satisfactory delimitation of these taxa. In view of these obstacles to accurate identification, it seems advisable to regard these infraspecific names as synonyms of *S. alterniflora* in accordance with Hitchcock (1935), Swallen (1939), and Chase (1950).

In the recent monographic study of the genus by Saint-Yves (1932), *S. alterniflora* is considered as *S. maritime* subsp. *glabra* St. Y. Under the subspecies, three varieties, four subvarieties, and one forma are recognized. Variety *brasiliensis* is considered discrete from the remainder on the basis of its pedunculate spikes and distribution in South America. As noted above, this feature is somewhat inconsistent in South American material and does not appear to be a satisfactory means of separation. Two subvarieties are proposed for var. *brasiliensis*, based upon the variable number of spikes. Three to eight spikes characterize subv. *fallax* and fifteen to twenty are typical of subv. *radii*. Examination of a number of South American specimens shows variation in spike number from two to eighteen without distribution into two distinct groups.

Variety *alterniflora* of Saint-Yves, distributed in North America and Europe, is supposedly separable from var. *glabra* (also distributed in North America and Europe) on the basis of spikelet length, said to be 12--14 mm in var. *alterniflora* and 9--11 mm in var. *glabra*. A second criterion is the relative lengths of the glumes. First glumes are supposedly shorter than or equal to one-half the length of the second in var. *glabra* and longer than one-half the length of the second in var. *alterniflora*. Lengths of the spikelets and glumes have been found to be quite variable throughout the species, but they do not show the correlation implied by the criteria of Saint-Yves.

Saint-Yves proposed two subvarieties for var. *glabra*. Subvariety *typica* is said to be separable from subv. *pilosa* by virtue of the glabrous spikelets and six to ten spikes. Pilose spikelets and three to five spikes are said to characterize var. *pilosa*. Study of the specimens from Europe and North America shows that spike number is not correlated with the variable pubescence of the spikelets. A forma *gracilis* is proposed for var. *alterniflora*. It is described as merely a slender form of the typical *alterniflora*. Saint-Yves states that specimens of var. *alterniflora* grade imperceptibly between the slender form and the typical.

Results of a critical analysis of the taxa proposed by Saint-Yves show

that the criteria for separating them are inconsistent; it therefore seems advisable to regard these names as synonyms of S. alterniflora Lois.

A hybrid, X S. merrillii, between S. alterniflora and S. cynosuroides was suggested by Chevalier (1933). The evidence for hybrid affinities exhibited by the "hybrid" is a greater number of spikes than ordinarily encountered in S. alterniflora. However, the type specimen (Bicknell 11300, Long Island, N.Y., NY) possesses two panicles, one with twenty-one spikes, the other with seven spikes. Duplicates cited by Chavalier were also examined. (Kearney, Long Island, N.Y., US, F; MacKenzie 7339, Leonardo N.J., 7501, Ocean City, N.J., NY; Ferguson 724, 725, 726, 759, Long Island, N.Y., NY). So far as can be determined, none of the specimens reveal any marked morphological dissimilarities between them and the remainder of the highly variable population. Spike number varies from three to twenty-five throughout the species. The "hybrids" may be nothing more than specimens with a greater number of spikes.

Distribution

As noted in the preceding discussion, this species ranges over the east coast of North and South America, England, and France. It has also been introduced, through oyster culture, into northwestern United States. Maps showing the distribution of the species are shown in Figs. 3, 4, 5. A single specimen is known from Guadeloupe, West Indies (Perottet, Antilles, Guadeloupe, 1842P; fragment in US).

The plant is normally one of the intertidal zone, inhabiting the muddy banks of lagoons which are subject to tidal activity. It is usually found in salt water habitats and often occurs in large, dense, pure stands that range from muddy permanent shore lines well out onto the strand. However, Fernald (1941) found the plant in fresh to brackish water sites along the James River, Virginia. In pure stands which were observed to stretch for over one hundred meters or more, some variation was observed in the height of the plant and in the vigor of the panicle. In some cases, very slender plants were found intermingled with the larger ones, but visual inspection showed that a continuous range of variation was present.

Perhaps the most striking feature of this species is its ability to bind soil along the coast. Rhizomes are thick, fleshy and are embedded quite deeply in the silt. The large air spaces in the rhizomes and the highly inflated scales doubtless aid this species in persisting in areas where little atmospheric oxygen is likely to be found in the soil. To the unhappy plant collector, the most striking thing about the plant in its native habitat is the strong, unpleasant odor that accompanies the dislodged culms. This noxious, sulphurous odor has persisted in some of the author's collections for nearly a year.

Flowering dates seem to be quite variable for this species. In North America, it flowers from June to October; in South America from December to June; and in Europe from July to November. Flowering seems to be somewhat erratic, for among Florida specimens examined in the field in early August, some inflorescences had emerged some time before and had been completely eaten away by insects, while others were still well enclosed within the leaf sheaths. Most New England plants examined in late August were at or beyond the peak of anthesis.

Fig. 3. Distribution of Spartina alterniflora in North America.

Fig. 4. Distribution of Spartina alterniflora in South America.

Fig. 5. Distribution of Spartina alterniflora in Europe.

5. SPARTINA FOLIOSA

Spartina foliosa Trin. Mem. Acad. St. Petrsbg. Sci. Nat. VI. 6:114. (1840) (Type in LE from California)
Spartina leiantha Benth. Bot. Voy. Sulph. 56. (1844) (Type in K from Baja, California)
Spartina densiflora Brong. var. typica St. Y. subv. brongniertii St. Y. forma acuta St. Y. Cand. 5:76. (1932) (Based on a specimen from Humboldt County, California deposited in the Delessert Herbarium, G)

Description (Plate II, g-h)

Culms to 1.5 meters tall, erect, terete, fleshy, glabrous, commonly with adventitious roots produced from the lower nodes, usually solitary or in small clumps, from widely spreading, more or less slender, flaccid, whitish rhizomes, the scales not closely imbricate; sheaths smooth, the lower somewhat wrinkled, margin of the orifice pilose; ligule a ring of hairs 1--2 mm long; blades flat to loosely involute, glabrous on both surfaces, margins glabrous to very sparingly scabrous, tip acuminate; panicle 12--25 cm long, usually cylindrical, often partially enclosed within the uppermost sheath; panicle axis 3--4-angled, flattened, twisted, glabrous; spikes 3--25, 2--8 cm long, the lower usually the longer, alternately to irregularly arranged, subremote below, becoming crowded toward the apex of the panicle, sessile, usually tightly appressed and often twisted, giving the panicle a cylindrical contour; rachis of the spikes glabrous, rarely prolonged beyond the terminal spikelet; spikelets 8--30, 8--25 mm long, alternate, appressed or occasionally spreading, moderately imbricate, often subremote on the lower spikes, not readily disarticulating; first glume linear, 6--12 mm long, often curved, usually more than one-half as long as the second, glabrous to sparingly pilose, keel glabrous to sparingly pilose above, glabrous to long-pilose at the base, tip acuminate to obtuse or rounded; second glume 8--25 mm long, often curved, glabrous to sparingly pilose, keel glabrous to sparingly pilose, glabrous to long-pilose at the base, margins glabrous to sparingly pilose, tip acuminate to blunt or rounded; lemma glabrous to sparingly pilose, keel glabrous, margins glabrous to sparingly pilose, tip obtuse, rounded or lobed; palea thin and papery, glabrous, tip acuminate, rarely rounded, slightly exceeding the lemma; anthers 3--6 mm long; somatic chromosome number 56.

Observations

Spartina foliosa is a rather uniform species. The vegetative features do not exhibit any peculiarities of taxonomic usefulness. Plants of this species seem to agree very closely in vegetative parts with other members of the same complex. The panicle, on the other hand, is strikingly different in several aspects. The spikes on a single panicle show definite variability in length. Basal spikes are usually much longer than the median. In addition, the lower spikes are much less closely imbricated along the panicle axis than are the upper ones. Numerous, tightly appressed spikes give the panicle a cylindrical contour. In this respect the species approaches a characteristic of Complex 1. The species

Fig. 6. Distribution of Spartina foliosa along the west coast of North America.

does exhibit some variability in panicle length, spike number and length, spikelet length and pubescence on the spikelets. However, none of the variations encountered could be correlated with geographic distribution or other morphological features in any way that would suggest population differences or differing levels of polyploidy. The octoploid chromosome number (2n = 56) has been reported for the species (Church, 1940).

Nomenclature

A fragment of the type specimen deposited in the United States National Herbarium was available for examination. There is no doubt of the accuracy of the typification.

The specimen upon which the name S. densiflora ... forma acuta St.Y. was based was not available for examination. Saint-Yves (1932) notes that Hitchcock had identified the specimen as S. foliosa with which it agreed in all particulars save spikelet length. This specimen possessed spikelets 7--8 mm long while the spikelet lengths in S. foliosa were, according to Saint-Yves, 12--16 mm. Spikelet lengths found during the present investigation range from 8--25 mm. The fact that the forma of Saint-Yves is based upon a single character which exhibits so much variability seems reason enough to reject the name and treat it as a synonym of S. foliosa. While habitat has not been shown to influence directly the size of spikelets, it may be that it does. In this case, it may be significant to note that the label of the specimen in question bears the information that it was collected in the drier part of the salt marsh at Eureka, California.

Distribution

Spartina foliosa appears to be limited to the Pacific coast of North America (Fig. 6). It occurs in the intertidal zone along the edges of the strand, in the salt marshes and in tidal lagoons. The plant flowers from July to November. The species does not seem to produce viable seed regularly. Labels accompanying collections from California indicate that ergotization of the ovary is of common occurrence.

6. SPARTINA LONGISPICA

Spartina longispica Haum. and Par. ex St. Y. Cand. 5:92. (1932) (pro hybr.) (Type in G from Pipinas, Argentina)

Description (Plate III, a-b)

Culms to 2 meters tall, erect, terete, often fleshy, glabrous, usually solitary from short, tough or elongate, flaccid rhizomes, the scales moderately imbricate; sheaths smooth to somewhat striate, the lower often wrinkled, glabrous, margin of the orifice glabrous, rarely pilose; ligule a ring of hairs 1--2 mm long; blades flattened below, becoming involute toward the apex, glabrous to scabrous on the adaxial surface, glabrous on the abaxial, margins glabrous to scabrous, tip acuminate; panicle 14--45 cm long, often partially enclosed within the uppermost sheath; panicle axis 3-angled, glabrous to sparingly scabrous on the edges; spikes 4--16, 4--18 cm long, 2--5 mm wide, alternate, loosely to closely appressed, usually pedunculate; rachis of the spikes glabrous to scabrous, rarely prolonged beyond the terminal spikelet; spikelets 10--35, 12--24 mm long, 1.5--2.5 mm wide, alternate, often tightly appressed, occasionally spreading, moderately imbricate, often pedicellate, the pedicel pilose; first glume linear, 6--12 mm long, about one-half the length of the second, glabrous to sparingly pilose, keel pilose to hispid, margins glabrous or very sparingly hispidulous, tip acuminate to obtuse; second glume 12--24 mm long, glabrous to sparingly pilose, keel pilose to hispid, margins glabrous or sparingly hispidulous, tip acuminate to obtuse; lemma glabrous to sparingly pilose, keel glabrous below, sparingly hispid or pilose above, tip acuminate, rounded or obtuse; palea thin and papery, glabrous, tip obtuse to acuminate; anthers 3--7 mm long.

Observations

Spartina longispica was described by Saint-Yves (1932). He considered it a hybrid between the intertidal S. brasiliensis and the dry-land S. montevidensis. Evidence with which Saint-Yves purported to show hybrid affinities was found in the nature of the rhizomes, the leaf blades and the inflorescence. The rhizomes of S. brasiliensis are long and flaccid. Rhizomes in S. montevidensis are wanting or very short. The intermediate condition, supposedly reflected by the hybrid is suggested by short, stolon-like rhizomes. Examination of the cross-section of leaf blades of the species concerned showed important evidence of hybridization. Differences were found in the amount and position of chlorenchyma within the leaf blades. Inasmuch as living material was not available, this portion of Saint-Yves work was not verified during the present investigation. Through a study of the inflorescences of the putative parents

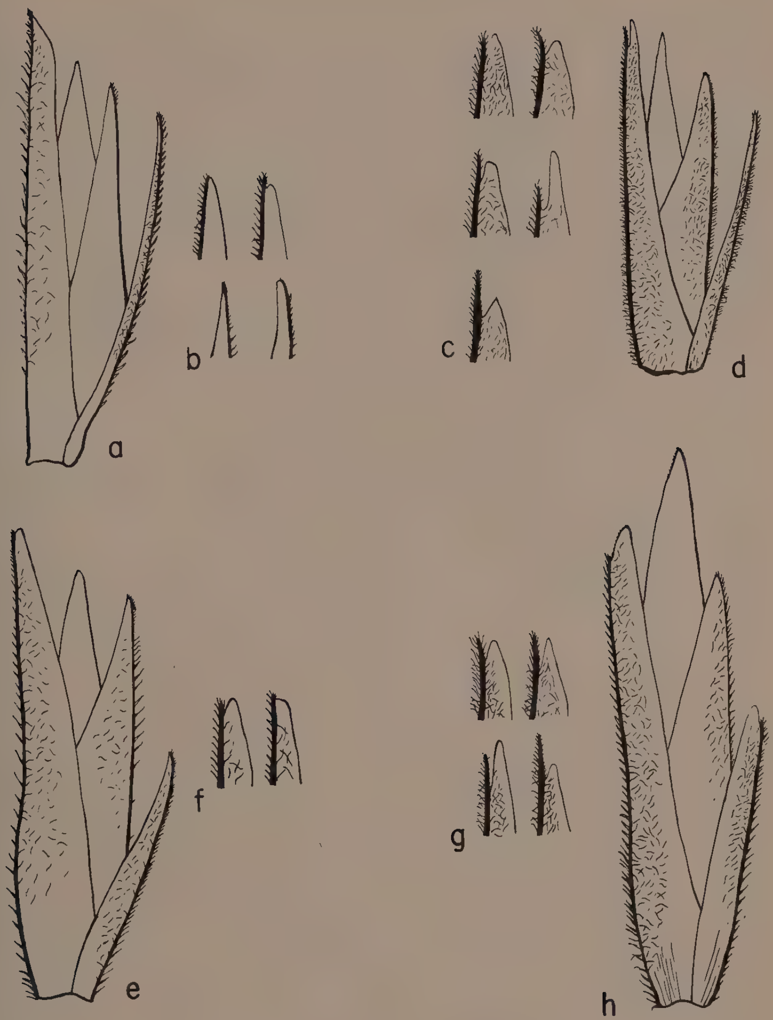

PLATE III

a-b. Spartina longispica. a. spikelet 3.75X, b. second glume tips 3.75X.

c-d. Spartina maritima. c. second glume tips 7.5X, d. spikelet 3.75X.

e-f. Spartina neyrautii. e. spikelet 3.75X, f. second glume tips 7.5X.

g-h. Spartina townsendii. g. second glume tips 3.75X, h. spikelet 3.75X.

and the hybrid, Saint-Yves claimed to have found differences which further suggested hybrid affinities. In S. brasiliensis, spikes were long and loosely appressed against the smooth panicle axis. Spikes of S. montevidensis were shorter and more or less tightly appressed against the axis which was smooth below and scabrous above.

Parodi (1937) maintained that the three species are found quite close together. He stated that S. brasiliensis occupies the intertidal zone, S. montevidensis the dry beach and S. longispica the intermediate habitat. S. montevidensis is thought to be separable from the other two on the basis of its much shorter spikelets (said to be 8--12 mm long), its sessile spikes and its lack of extensive rhizomes. S. brasiliensis is supposedly separable from S. longispica on the basis of its longer spikelets. Spikelet lengths of 15--18 mm are given for S. brasiliensis while lengths of 12--14 mm are given for S. longispica. The rhizomes of the latter two are also shown to differ in accordance with Saint-Yves' distinctions given above.

The name S. brasiliensis and S. montevidensis by which Saint-Yves and Parodi have referred to the two putative parents have been shown in this paper to be synonyms of S. alterniflora and S. densiflora respectively. Hereinafter, the two parent species will be referred to by the latter binomials.

At first glance the hypothesis presented by Saint-Yves and Parodi seems quite plausible, but there are certain inconsistencies. Many specimens previously identified as either S. alterniflora (S. brasiliensis) or S. longispica do not answer to their criteria. The pubescence causing scabridity on the panicle axis is quite variable and does not seem to be correlated with appression of the spikes. Spikelet lengths from the same plants may show a variation from 13--16 mm in length. In addition, certain specimens identical with regard to spikelet length differ in the type of rhizomes. In some they are hard, short, and knotty, and in others long and somewhat flaccid, more or less typical of S. alterniflora. In short, identification of plants at hand is fraught with exceeding difficulty.

A possible explanation for the numerous plants which fail to fulfill the criteria proposed is that they are individual hybrid progenies which, because multiple factors are involved, segregate out along more or less of a gradient toward either parent, or that they are simply backcrosses to either parent and, as a result, stand somewhat intermediate between the putative F_1 hybrid and the original parent. A combination of the two preceding alternatives might also be involved. If these conditions were true one might expect a rather continuous range of variations from one parent to the other. Such, however, is not the case, for S. densiflora is discretely separable from the others on several counts, while the more puzzling specimens seem to be variously disposed between the putative hybrid and the intertidal S. alterniflora. Therefore some other explanation must be sought.

It became apparent to this investigator after considerable study of the problem that some plants previously identified as S. alterniflora (S. brasiliensis) were not actually S. alterniflora at all, but were members of another population altogether. This population is similar to S. alterniflora in many respects, but the panicle is obviously much more robust. In connection with geographic distribution, a curious fact was brought to

light. This group of more robust specimens, which included those previously identified as hybrids, were localized at or near the mouth of the River Plate, while virtually all of the less robust true S. alterniflora were distributed further northward along the coast.

The plants of the River Plate population are not easily separated from S. alterniflora by means of any single key character but, as will be shown in connection with the study of the hybrid origin of the population, certain quantitative indices may be successfully employed. Accordingly, this discrete population is named S. longispica.

The hypothesis of the hybrid origin of S. longispica advanced by Saint-Yves (1932) and corroborated by Parodi (1937 and in personal communication) is not without merit. However, it seems evident that what they were attempting to define as hybrids are perhaps ecological variants of what may be a larger hybrid population. The fact that plants with short, hard rhizomes are found in the intermediate habitat may be an indication that environmental conditions influence the ultimate size and conformation of rhizomes.

In an effort to explore more fully the conclusions drawn by Saint-Yves (1932) regarding the hybrid origin of S. longispica, a hybrid index was constructed according to methods described by Anderson (1936, 1949) and Larisey (1940). A number of characters were selected by which the putative parent populations may be distinguished. Several of these characters serve to separate the parents discretely but the remainder reflect only the general trends of the populations, the extremes overlapping somewhat. An index value of 0 was given to a particular character if it was typical of S. alterniflora, while a value of 2 was assigned if it more closely represented S. densiflora. In several of the features used to separate the parent populations, an intermediate condition was found. This intermediate was given a value of 1. A total of 14 characters were selected, the values of which, for any single specimen, when added together provided a minimum total value of 0 for S. alterniflora and a maximum total value of 28 for S. densiflora.

This index was constructed solely from features discernible in herbarium specimens; living material was not available. Thus, certain characters which may actually offer a means of separation of the putative parents were not used because they were not always present on the herbarium sheets. This was particularly true of the basal portion of the culms and the rhizomes.

The 14 characters used in the construction of the hybrid index follow:

1. The leaf blades of S. alterniflora are normally flat, becoming somewhat involute near the apex. This latter feature is no doubt accentuated by drying. On the other hand, leaves of S. densiflora are decidedly involute throughout the length of the blade. An intermediate condition is suggested in several of the putative hybrids by a flattened base becoming markedly involute a short distance above the base. Since field observations were not made on these specimens it is entirely possible that this suggested intermediate condition is purely an artifact.

2. A great majority of the specimens from South America referable to S. alterniflora have rather long-peduncled spikes. Some specimens

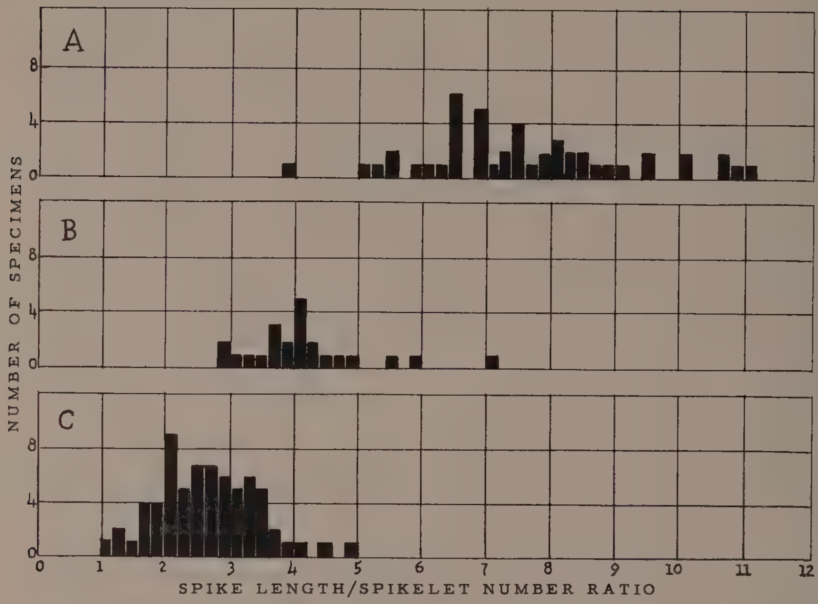

Fig. 7. Distribution of Spikelet Imbrication Values
A. Spartina alterniflora. B. Spartina longispica. C. Spartina densiflora.

may have lower spike peduncles as long as 5 cm. In the case of S. densiflora the spikes are sessile. The intermediate condition may be present in the putative hybrids in which the peduncles of some of the lower spikes vary from 0.5--1.5 cm in length.

3. Spikes of S. alterniflora are more or less the same length from base to apex of an individual panicle. In contrast, the panicles of S. densiflora usually have rather elongate basal spikes with a perceptible diminution in spike length toward the apex.

4. During the dissection of spikes and spikelets, it was observed that spikelets of S. densiflora disarticulate rather readily from the rachis, while those of S. alterniflora are somewhat persistent. The condition does not appear to be universally true among specimens of S. alterniflora, but reflects only the general trend of the population. Spikelets of all the specimens referred to the putative hybrid disarticulated readily.

5. In South American specimens of S. alterniflora, the spikelets are noticeably less crowded along the axis of the spike. A numerical evaluation of this imbrication of spikelets is presented in Fig. 7A. A similar evaluation of the more densely imbricate S. densiflora is presented in Fig. 7C. The values are obtained by calculating a ratio of the spike

length to the number of spikelets on the median spike. Comparison of the two histograms shows that there is some overlap making the feature an unsatisfactory key character, but it also shows that general trends in the population differ to a considerable extent. The values for most of the putative hybrids fall near the center of the range of overlap (Fig. 7B). Accordingly, any specimen which showed a value between 3.5 and 4.5 was scored as an intermediate.

6. Spikelets may be slightly pedicellate in S. alterniflora while they are sessile in S. densiflora. Again, this character does not appear to be constant throughout but is a more or less general trend in the specimens examined. Because the lengths of pedicels in S. alterniflora varied throughout a range of only 0--2 mm, no attempt was made to define an intermediate.

7. Somewhat spreading spikelets are typical of S. alterniflora while complete appression of spikelets characterizes S. densiflora. Most of the putative hybrids have spikelets rather tightly appressed to the rachis.

8. The relative length of first and second glumes may be used to separate the parent populations, although individual variation within both species precludes its use as a key character. S. densiflora commonly possesses first glumes that are shorter than one-half the length of the second, while S. alterniflora first glumes are usually longer than one-half the length of the second. No attempt was made to define an intermediate, although in several specimens first glumes exactly half as long as the second were observed.

9. The pubescence on both glumes has been found to be a useful taxonomic character separating the putative parents. That of S. alterniflora consists of trichomes that are rather soft and somewhat flexible and of varying lengths and distribution (Plate II, a-f). Trichomes of S. densiflora, on the other hand, are uniformly short and rigid (Plate IV, i-k). The trichomes of several putative hybrids seemed to be somewhat more rigid than those of S. alterniflora and slightly longer than those of S. densiflora. These were scored with a value of one.

10. The tip of the first glume in S. densiflora is rather obtuse while that of S. alterniflora is acuminate (Plates II, a-f; IV, i-k). The greater majority of the specimens examined show this condition to hold quite generally. The putative hybrids, for the most part, answered to the S. alterniflora type.

11. The same feature was observed at the tip of the second glume although the conditions were reversed. The second glume tip of S. densiflora is acuminate but not awned. That of S. alterniflora is obtuse, rounded or somewhat toothed with the mid-nerve projecting slightly beyond the toothed margin. Plates II, a-f and IV, i-k show the common type of second glume tips encountered. The putative hybrids exhibited about as much variability as S. alterniflora.

12. In most of the South American specimens of S. alterniflora, the lemmas were observed to be more or less glabrous on the keel. Occasionally a few trichomes are present near the tip. The keel of the lemma in S. densiflora is hispidulous on the upper two-thirds. Most of the putative hybrids are pubescent on the upper two-thirds of lemma keel, although the trichomes are, in general, somewhat longer than those encountered in S. densiflora. The distinction between putative parents was based solely on the distribution of the trichomes.

13. The texture of the glumes appears to be a feature in which the putative parents differ somewhat. S. alterniflora second glumes are somewhat thin and papery and tend to be rather pliable. Those of S. densiflora are slightly thicker and somewhat indurated. The putative hybrids agreed for the most part with S. densiflora in this respect.

14. The tip of the palea in S. densiflora is acuminate, occasionally possessing trichomes along the two rather closely set nerves which converge near the tip. On the other hand, the tip of the palea in S. alterniflora is obtuse to rounded and lacks pubescence. Attempts to define an intermediate failed here, although considerable raggedness was observed in some of the palea tips of the putative hybrids. They were scored, however, as typical of S. alterniflora.

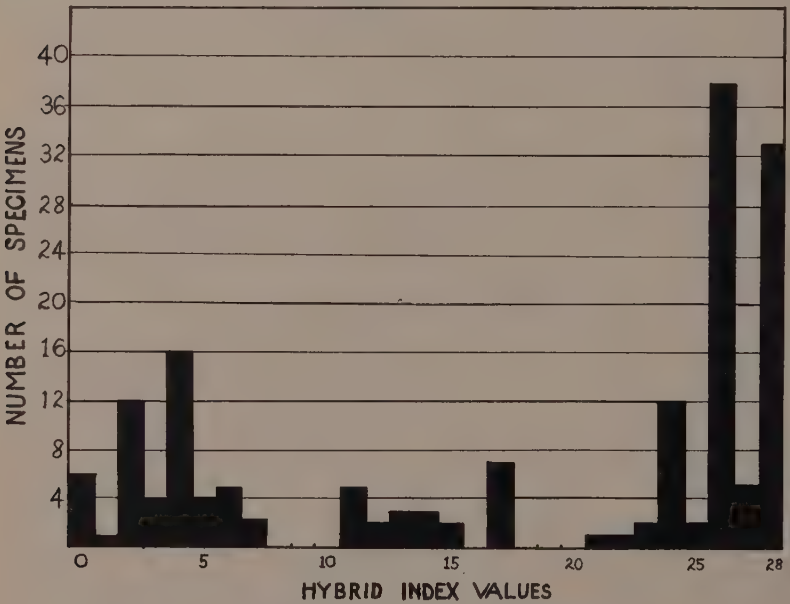

Fig. 8. Distribution of Hybrid Index Total Scores.

A total of 171 specimens were scored according to the features above. Results of the scoring are presented in Fig. 8. All the specimens within the intermediate cluster (11-17) were collected from the mouth of the

River Plate or near it. It should be noted that among plants within the intermediate cluster are specimens which had been identified by Parodi as S. brasiliensis (S. alterniflora) as well as several identified by him as S. longispica.

The specimens comprising this intermediate cluster are referable to S. longispica. From the evidence presented, they appear to be separable from both parents. Additional evidence showing that the S. longispica is discrete from S. alterniflora will be presented in this paper in the section dealing with distinctions between South American species of Spartina.

S. longispica, as defined in this paper, does have some characteristics which appear to relate it to S. densiflora. The ability to tolerate a dry land habitat is not known for any segment of S. alterniflora; yet it is shown by some specimens of S. longispica.

Two other features suggesting hybridization which do not lend themselves to treatment within the framework of the hybrid index are panicle and leaf length. Differences in these characters exhibited by S. longispica and S. alterniflora may be evidence of hybrid vigor. Measurements made on lengths of panicle and the second leaf from the summit are presented in Table 5. Panicle width measurements were found to be of little value, since pressing for herbarium storage often flattens and widens an otherwise narrow panicle.

Table 5. Lengths of panicle and blade in S. alterniflora and S. longispica.

	S. alterniflora		S. longispica	
	Leaf	Panicle	Leaf	Panicle
Number of specimens	23	27	17	22
Minimum length (cm)	9.0	8.0	17.0	14.0
Average length "	17.6	15.6	29.5	28.0
Maximum length "	35.0	30.0	44.0	44.0

While the obvious overlap precludes use of the panicle and leaf length as key characters, there appears to be a significant difference in the average values for the two populations.

It is entirely possible that what is discussed here as a putative hybrid may not be a hybrid at all. There can be little doubt that the specimens from the area of the River Plate represent a population somewhat discrete from S. alterniflora. Further, it would appear from the evidence presented that some characteristics resembling S. densiflora actually appear in S. densiflora. This immediately suggests hybrid affinities or at least gene flow from S. densiflora to the extremely localized population.

It seems highly improbable, in view of the limited distribution, that hybridization is of common occurrence. Certainly concomitant distribution of the putative parents over extensive areas of the Brazilian coast offers ample opportunity for the frequent occurrence of hybridization. Yet, the putative hybrid population is extremely limted in its distribution.

A more likely explanation is that the entire population (both intertidal and intermediate zone plants) are the results of a single hybridization and that the resultant hybrid has proved fertile, or that the plant reproduces vegetatively so vigorously it has invaded territory which once may have been occupied by S. alterniflora and more or less obliterated it from the region. The case recalls that of the highly vigorous S. townsendii.

No specimens of S. alterniflora from the region occupied by the putative hybrid are deposited in any of the herbaria consulted during the course of this investigation. All specimens from that area had been previously identified as S. brasiliensis or S. alterniflora were distinctly referable to S. longispica.

The index described above, while useful for separating the three species involved, may not actually represent an accurate analysis of the supposed hybridization. If, as has been suggested, the hybridization occurred only once, then the index may be quite out of line in its utilization of trends in a variable population as bases for comparisons. Obviously, out of the two variable putative parent populations the individual plants which went into the formulation of the putative hybrid cannot be known.

Nomenclature

The population as delimited by Saint-Yves (1932) was thought to be of hybrid origin. It was designated X Spartina longispica. Parodi (1937) elected to regard it as a discrete species and dropped the hybrid symbol. However, he did retain the original author citation, viz. S. longispica Haum. and Par. apud Saint-Yves, but neglected to indicate that the rank of the taxon was altered from hybrid to species. Under articles 59 and 60 of the International Code of Botanical Nomenclature, which would seem to apply in this case, the name is correctly cited Spartina longispica (Haum. and Par. ex Saint-Yves) Par. (pro hybrid).

Distribution

S. longispica has a rather limited distribution. It exists only at the mouth of the River Plate in both Argentina and Uruguay.

The habitat of S. longispica also has been suggested in the preceding observations. While the intertidal zone appears to be the primary habitat, it nonetheless has been shown to invade the drier portions of the beach zone. Collecting dates indicate that the plants flower from January to May.

7. SPARTINA MARITIMA

Spartina maritima (Curt.) Fern. Rhod. 18:180. (1916)
Spartum essexianum, spica gemina clausa Petiver, Gram. Concordia 1. (1716) (Type unknown)
Dactylis cynosuroides Loefl. Iter Hisp. 115. (1758) non Dactylis cynosuroides L. (1753) (Type from Lusitania)
Dactylis maritima Curt. Enum. Br. Gr. 4. (1787) non Dactylis maritima Walt. (1788) (Based on Spartum essexianum, spica gemina clausa Petiver)
Dactylis stricta Ait. Hort. Kew. 1:104. (1789) (Type from England)
Spartina stricta (Ait.) Roth, Neue Beitr. 101. (1802)

Paspalum cynosuroides (Loefl.) Brot. Fl. Lusit. 83. (1804)
(Based on D. cynosuroides Loefl.)
Trachynotia stricta (Ait.) DC. Fl. Fr. 3:74. (1805)
Limnetis pungens Rich. ex Pers. Syn. Pl. 1:72. (1897)
(Based on D. stricta Ait.)
Spartina pungens (Rich.) Beauv. Nouv. Agrost. 25. (1812)
Spartina capensis Nees, Fl. Afr. Austr. 260. (1841)
(Type from South Africa)
Spartina maritima (Curt.) Fern. subsp. stricta (Ait.) St. Y. Cand. 5:45. (1932) (Based on D. maritima Curt.)

Description (Plate III, c-d)

Culms to 0.8 meter tall, erect, terete, glabrous, solitary or in small clumps from widely spreading, slender rhizomes, scales not closely imbricate; sheaths smooth to striate, the lower very often wrinkled, glabrous, margin of the orifice glabrous to very sparingly pilose; ligule a ring of hairs about 0.5 mm long; blades short, not exceeding 12 cm in length, more or less loosely involute, readily disarticulating from the sheath, glabrous to very sparingly scabrous on the adaxial surface, glabrous on the abaxial, margins glabrous, tip acuminate; panicle 4--14 cm long; panicle axis flattened, rounded or obscurely 3-angled, glabrous; spikes 1--7, commonly 2, 2--11 cm long, alternate, loosely appressed, moderately imbricate, sessile; rachis of the spikes glabrous, often prolonged beyond the terminal spikelet; spikelets 5--30, 10--15 mm long, alternate, loosely appressed to spreading, not closely imbricate; first glume narrow, 7--10 mm long, usually longer than one-half the second, densely pilose, keel pilose, margins glabrous, tip acuminate to obtuse or rounded; second glume 10--15 mm long, densely pilose, keel pilose, margins glabrous, tip acuminate, rarely obtuse; lemma densely pilose, keel pilose above, glabrous below, margins glabrous, tip obscurely lobed; palea thin and papery, glabrous, tip acuminate; anthers 4--6 mm long; chromosome number 56.

Observations

This species, limited to the Old World, is rather uniform. While it has attained a wide distribution ranging from the British Isles to South Africa, it is still remarkably uniform both vegetatively and in the inflorescence. The greatest variation is in the number of spikes, where as many as seven can be found. The predominant number is two--hence one of its common names, Two-spiked Cocksfoot Grass.

The octoploid chromosome number of 56 in plants from the British Isles has been reported by Huskins (1931). Specimens from the Mediterranean and South African segments of the range have not been cytologically analyzed.

Nomenclature

Curtis (1787) published the name Dactylis maritima and this epithet becomes the basis for the present combination of Fernald (1916), who clearly states the case for the ascription of the name. Although the publication of Curtis was in the briefest possible form, and did not itself contain a description of the species, it gave a clear reference to Ray

(1724) as the source for the description. Ray's description is based on *Spartum essexianum, spica gemina clausa* of Petiver (1716)

Aiton (1789) described a specimen from England as *Dactylis stricta*. Roth (1802) recognized its affinities with the genus *Spartina* and accordingly published the combination *Spartina stricta*. This combination was in constant use for over a century. Only the most recent European works, viz. Clapham, Tutin, and Warburg (1952) have recognized the proper recombination of names as given by Fernald (1916).

Distribution

Spartina maritima is distributed exclusively in the Old World from the Netherlands and England south to the Cape of Good Hope along the Atlantic Seaboard. It has apparently become adventive at the head of the Adriatic Sea. Little is known of its distribution in Africa. Fig. 9 shows the distribution of the specimens examined.

The species appears to be limited to salt water habitats, on the strand or in tidal bays and lagoons. It does not seem able to withstand aggression by the more vigorous *S. townsendii* (Arber, 1934; Oliver, 1925), and in regions around Poole Harbor, England, it is being obliterated by *S. townsendii*. Collecting dates indicate that the species flowers from June to November in Europe and in February in South Africa.

Fig. 9. Distribution of *Spartina maritima* in Europe and Africa.

8. SPARTINA NEYRAUTII

Spartina neyrautii Fouc. Ann. Soc. Nat. Rochelle. 8. (1894)
(Type from Basse-Pyrenées)

Description (Plate III, e-f)

Culms to 1 meter tall, erect, terete, glabrous, usually solitary or in small clumps, from widely spreading, more or less slender rhizomes, scales not closely imbricate; sheaths striate, glabrous, margin of the orifice glabrous to short-pilose; ligule a ring of hairs 0.5--1 mm long; blades elongate, flattened, becoming involute toward the apex, glabrous on both surfaces, margins glabrous, tip acuminate; panicle 15--20 cm long, less than 5 mm wide; panicle axis 3-angled, glabrous; spikes 4--6, 8--12 cm long, alternate, tightly appressed, moderately imbricate, pedunculate, peduncles about 1 cm long; rachis of the spikes glabrous, not often prolonged beyond the terminal spikelet; spikelets 10--25, 14--16 mm long, alternate, tightly appressed, not closely imbricate, often pedicellate; first glume linear, 8--12 mm long, usually longer than one-half the second, pilose, keel sparingly pilose, margins glabrous, tip acuminate to obtuse, second glume 14--16 mm long, pilose, keel pilose, margins glabrous, tip usually bilobed; lemma glabrous to sparingly pilose above, keel pilose above, glabrous below, margins glabrous, tip acute, obtuse, rounded or obscurely lobed; palea thin and papery, slightly exceeding the lemma, tip acuminate to rounded; anthers 3--6 mm long.

Observations

Spartina neyrautii, like S. townsendii, has been adjudged a hybrid between the endemic European S. maritima and the introduced and variable S. alterniflora. Arber (1934) suggested that the two hybrids may have arisen in like manner, and that one may simply be the reciprocal of the other. Although the two populations have been considered identical by Saint-Yves (1932) and Chevalier (1923), Jovet (1941) has pointed to differences in the ligule and second glume tip by which the two may be effectively distinguished. Additional evidence in support of Jovet's contention is presented in a succeeding section of this paper dealing with means for separating and identifying species.

To date, cytological evidence supporting the hypothesis of the hybrid origin of S. neyrautii has not been published. In the absence of cytological findings, it is difficult to assess the origin of the species. That it combines characters of both S. maritima and S. alterniflora is evident. Pilosity of the glumes relates it to S. maritima while lack of early blade abcission may show it to be allied to S. alterniflora. Further evidence in support of hybrid origin for the species is found in its highly restricted distribution within a small segment of a larger area occupied by both putative parents.

Of particular importance to the resolution of the S. neyrautii problem is the nature of S. alterniflora distributed within the area now occupied by the hybrid. As shown in connection with observations on that species, all the specimens from southwestern France tend to be considerably less robust than those typical of the region around Southampton, England. That introduction of a different cytological segment of S. alterniflora

occurred suggests itself immediately. The less robust plants from southern France are not unlike those from America which have been shown by Church (1940) to have a somatic chromosome number of 56. It is therefore tentatively suggested that S. neyrautii, when cytologically examined, may be found to have a chromosome number quite different from that now known for S. townsendii. The fact that S. neyrautii is distinctly more slender, has generally more narrow spikes and shorter spikelets points to an obvious difference between the two species, somewhat more complex than that suggested to be due to reciprocal crosses.

Nomenclature

The description of S. neyrautii by Foucaud (1894) was written after study of specimens collected by E. J. Neyraut from Hendaye, France in 1892. No mention is made of a type specimen, and its whereabouts at the present time is unknown. However, duplicates of the Neyraut collection (E. J. Neyraut 3598, Hendaye,France, GH, US, and F) were examined.

Distribution

Specimens examined during the course of this study are shown by open circles in Fig. 10. The species is known only from a single station (Hendaye) in southwestern France. S. neyrautii occurs in salt marshes. While little is known of its ecology. it does not appear to be nearly so vigorous and aggressive as the closely related S. townsendii. The species has been observed to flower in August.

Fig. 10. Distribution of Spartina neyrautii and Spartina townsendii in Europe.

9. SPARTINA TOWNSENDII

Spartina townsendii H. and J. Groves. Bot. Exch. Club Rept. 37. (1881) (Type from Southampton, England; isotype in K)

Description (Plate III, g-h)

Culms to 1.5 meters tall, erect, terete, glabrous, solitary or in clumps from widely spreading thickish rhizomes, scales not closely imbricate; sheaths smooth to striate, the lower often wrinkled, glabrous, margin of the orifice pilose; ligule a ring of hairs 1.5--3 mm long; blades elongate, flat, becoming involute toward the apex, glabrous on both surfaces, margins glabrous, tip acuminate; panicle 15--30 cm long, more than 8 mm wide, shorter and narrower in dwarf forms; panicle axis 3-angled, glabrous; spikes 3--10, 10--20 cm long, rarely longer, shorter in dwarf forms, alternate, loosely appressed, moderately imbricate, usually pedunculate, peduncle about 1 cm long; rachis of the spikes glabrous, prolonged beyond the terminal spikelet; spikelets 10--30, 16--22 mm long, alternate, not tightly appressed nor closely imbricate; first glume linear, 8--14 mm long, usually more than one-half as long as the second, pilose, keel pilose, margins glabrous to very sparingly hispidulous, tip acuminate; second glume 16--22 mm long, pilose, keel pilose, margins glabrous to sparingly hispidulous, tip acuminate to obtuse; lemma pilose, keel pilose above, glabrous below, margins glabrous, tip obtuse, rounded or obscurely lobed; palea thin and papery, glabrous, often exceeding the lemma by as much as 2 mm, tip acuminate; anthers 7--9 mm long; somatic chromosome number 126.

Observations

There now seems to be general agreement among European botanists that S. townsendii is a distinct species. The most recent treatment, that of Clapham, Tutin and Warburg (1952), recognizes it as discrete from other species of the genus occurring in England.

The origin of S. townsendii has received considerable attention in recent years as a striking example of a new species having arisen within the period of man's civilization. The actual mechanics of the origin of this species were worked out by Huskins (1931). The story is essentially complete except for certain facets which may never be known. Dobzhansky (1937) and Arber (1934) present excellent detailed reviews of the process.

Essentially, S. townsendii is regarded as a hybrid between the endemic European S. maritima and the introduced and variable American S. alterniflora. The haploid chromosome number of S. maritima is 28, while that of S. alterniflora is 35. Fertilization may have resulted in the formation of a zygote with 63 chromosomes, which then doubled immediately to produce a plant with a somatic number of 126 chromosomes. Huskins (1931) has shown that with the somatic chromosome number for S. townsendii is 126. Of the many possible alternatives explaining the mechanism of origin of polyploidy in this case, the one presented above seems the most likely. The rather uniform nature of S. townsendii leads to the conclusion that hybridization has probably taken place but once. Further light is shed by the fact that S. townsendii has been shown,

according to Oliver (1925) and Arber (1934), to be vigorously aggressive both by means of fertile seed production and vegetative reproduction.

As noted above in the discussion of S. alterniflora, two levels of polyploidy exist within that species; the form with fifty-six chromosomes may be somewhat less vigorous than that with seventy. Observations on the variability of specimens of S. alterniflora from England, indicate that plants of both polyploid levels may be present there. Huskins (1931) has shown that the form with seventy chromosomes is present in England. This form seems to have been the one involved in the hybrid origin of S. townsendii.

The apparently stable polyploid is remarkably uniform in virtually all morphological features. Several of these show great usefulness as taxonomic key characters. Among these are ligules over 1.5 mm, spikelets over 15 mm, palea exceeding the lemma by 2 mm or more, and median spikes usually exceeding 10 cm. Other features which have been found useful but somewhat variable are the length of that part of the median spike rachis prolonged beyond the apex of the terminal spikelet, and length and width of the panicle. These features will be discussed in greater detail in the section of this paper dealing with the distinctions between species.

Certain anomalous plants have been found within this otherwise stable population. Chater and Jones (1951) describe two such anomalies. One is a dwarf form with much reduced spike and panicle length, fewer spikelets and brown color. The other is somewhat of a dwarf, differing from the normal in that the mid-portions of leaves contain a band of yellow tissue along the length of the blade. Chater and Jones do not provide nomenclatural status for these anomalies. They suggest that the anomalies may represent "disintegration" of the stable polyploid.

Nomenclature

The whereabouts of the holotype of Spartina townsendii is unknown. An isotype in the Kew Herbarium was not available for study. However, the description (H. and J. Groves, 1881) verifies the accuracy of typification.

Distribution

Fig. 10 shows the distribution of specimens examined. That the species is spreading rapidly by natural means is borne out by Arber (1934). S. townsendii is perhaps the most economically valuable member of the genus as attested by its introduction into many parts of the world for use in tideland reclamation.

Considerable literature dealing with the ecological relationships of S. townsendii has been published. Among the papers are those of Oliver (1925), Arber (1934), and Stapf (1908). The plant is largely one of the intertidal zone with a six-hour tolerance of submergence under salt water. It flowers from July to November and in November may often be found, according to Arber (1934), with sprouting seeds still clinging to the spikes. Of particular interest is its very aggressive nature by means of which it has invaded the territory once occupied by S. maritima and S. alterniflora and has obliterated them from the immediate area.

10. SPARTINA BAKERI

Spartina bakeri Merr. Bull. U.S. Dept. Agric. Pl. Ind. 9:14. (1902)
(Type in US from Lake Ola, Tangerine, Florida)
Spartina juncea Willd. var. bakeri (Merr.) St. Y. Cand. 5:91. (1932)
(Based on S. bakeri Merr.)

Description (Plate IV, a-b)

Culms to 2 meters tall, erect, terete, indurate, glabrous, in large, dense clumps from hard, knotty bases, rhizomes wanting; culms often with shoots from the lower nodes; sheaths smooth to striate, glabrous, the margin of the orifice glabrous; ligule a ring of hairs 0.5--2 mm long; blades elongate, usually involute, rarely flat, scabrous on the adaxial surface, glabrous on the abaxial, margins scabrous, tip acuminate; panicle 8--25 cm long; panicle axis 2--4-angled, flat, scabrous on the angles; spikes 3--16, 2--6 cm long, alternate, appressed, rarely spreading, moderately imbricate, sessile, the lower often short pedunculate; rachis of the spikes glabrous to sparingly scabrous on the angles; spikelets 10--30, 6--9 mm long, alternate, tightly appressed, closely imbricate; first glume linear, 3--6 mm long, shorter than one-half the second, keel hispid, margins sparingly hispidulous, tip acuminate; second glume 6--9 mm long, hispidulous, keel hispid, margins hispidulous, 2--3 lateral nerves, prominent, on one side of the second glume, tip acuminate; lemma glabrous, keel hispid, margins glabrous to very sparingly hispidulous, tip acute to obtuse or obscurely lobed; palea thin and papery, glabrous, tip acute to rounded, slightly exceeding the lemma; anthers 5 mm long; somatic chromosome number 42.

Observations

From the standpoint of morphology of the inflorescence, Spartina bakeri is hardly separable from S. patens. However, because of its unique vegetative habit and tolerance of fresh water it is quite distinct. Rhizomes are not produced as they are in S. patens. The culms grow in dense tufts up to several feet across, a feature which serves to set this species apart from its closely related congeners. While the inflorescence exhibits some variability in its parts, it is overlapped in every respect by S. patens. Consequently, herbarium specimens are extremely difficult of identification unless the collector has noted the peculiar habit on the label.

A characteristic feature of the inflorescence is the rather tight appression of the spikes. This feature was observed on all the specimens examined and is doubtless typical of the species. Its use as a good taxonomic key character is precluded by the presence of the same degree of appression by spikes of immature specimens of S. patens.

The only chromosome count reported for the species is that of Church (1940) wherein he gives 42 as the diploid number.

Nomenclature

Merrill (1902) recognizes Spartina bakeri as separable from other species of the genus on the basis of the unique vegetative habit. Unfortunately, the type specimen is without the basal portion of the culm and

underground parts. However, Merrill's description, evidently based upon additional plants and field observations by the collector (Baker), leaves no doubt as to the accuracy of the typification.

Saint-Yves (1932) treated the species as a variety of Spartina juncea. Doubtless S. bakeri is closely related to S. patens (S. juncea) and were it not for the complete absence of rhizomes and the ability of the plant to tolerate and invade fresh water sites, there would be little argument for its retention as a separate species.

Distribution

The species is quite successful in fresh water habitats. It is found along the sandy beaches and shores of many of Florida's inland lakes. Distributional data also show that it grows equally as well in salt water sites in Florida and southern Georgia. Collecting dates point to a rather erratic flowering by this species. Unlike other North American spartinas, this species flowers for the most part from December to May, but is occasionally found in flower during the summer.

11. SPARTINA X CAESPITOSA

Spartina X caespitosa (A.A. Eaton) Fern. Gray's Man. Bot. ed.8. 180. (1950) (Based on S. caespitosa A.A. Eaton)
Spartina caespitosa A.A. Eaton. Bull. Torrey Club. 25:338. (1898) (Type in GH from Seabrook, N.H.)
Spartina patens var. caespitosa (A.A. Eaton) Hitchc. Rhod. 8:210. (1906) (Based on S. caespitosa A.A. Eaton)
Trachynotia caespitosa Ait. in St.Y. Cand. 5:92. (Error for S. caespitosa A.A. Eaton)

Description (Plate IV, c-d)

Culms to 1.2 meters tall, slender, erect, terete, glabrous, in dense caespitose clumps without rhizomes or with short rhizomes and with short, extra-vaginal shoots from the base, or solitary from widely spreading, thick rhizomes, scales closely imbricate; sheaths smooth to striate, glabrous, margin of the orifice glabrous to short-pilose; ligule a ring of hairs 0.5--1.0 mm long, rarely longer; blades elongate, involute or flat, narrow, glabrous or scabrous on the adaxial surface, glabrous on the abaxial, margins glabrous or scabrous, tip acuminate; panicle 9--20 cm long; panicle axis 3-angled, scabrous on the angles; spikes 3--9, 3--9 cm long, alternate, appressed or spreading, usually pedunculate; rachis of the spikes scabrous on the angles; spikelets 20--50, 10--17 mm long, alternate, tightly appressed, closely imbricate; first glume linear 4--9 mm long, glabrous to sparingly hispidulous, keel hispid, tip acuminate or awned; second glume 10--17 mm long, glabrous to sparingly hispidulous, keel hispid to pectinate, lateral nerves prominent, one on either side of the keel, or 2--3 on one side of the second glume, tip acuminate or awned; lemma glabrous to sparingly hispidulous, keel glabrous or hispid only at the tip or hispid to pectinate on the upper three-fourths, margins usually hispidulous, tip obtuse, rounded, obscurely lobed, or apiculate; palea thin and papery, glabrous, bilobed and obtuse or rounded

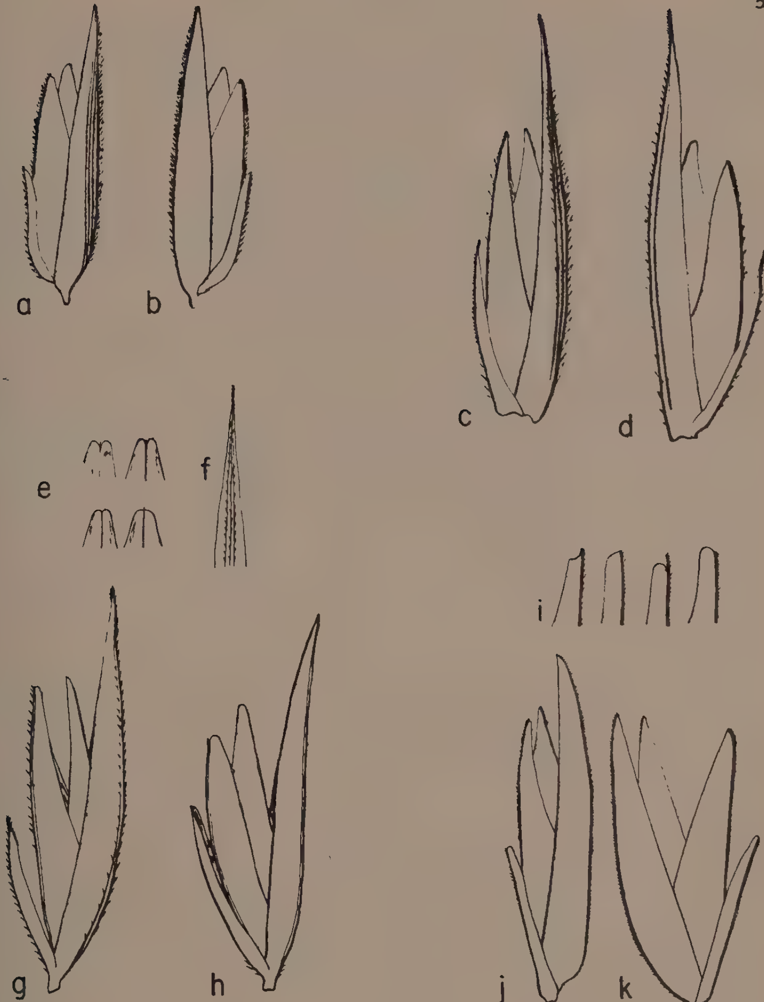

PLATE IV

a-b. Spartina bakeri.	a. spikelet showing lateral nerves 7.5X, b. same spikelet, opposite view 7.5X.
c-d. Spartina X caespitosa.	c. spikelet showing two lateral nerves 7.5X, d. Spikelet showing one lateral nerve 7.5X.
e-h. Spartina cynosuroides.	e. lemma tips, keel view 3.75X, f. second glume, keel view 3.75X, g, h. spikelets 3.75X.
i-k. Spartina densiflora.	i. first glume tips 7.5X, j-k. spikelets 3.75X.

at the tip, slightly exceeding the lemma; anthers 3--6 mm long; chromosome number 42.

Observations

The taxonomic position of S. caespitosa has been the subject of some controversy since it was first described by Eaton (1898). Hitchcock (1906) reduced it to varietal rank under S. patens. Swallen (1939) retained it as a valid species as did Chase (1950). Fernald (1950) relegated the plant to a hybrid category, suggesting that it showed a combination of characters from both S. pectinata and S. patens.

Church (1940) had earlier hypothesized a hybrid origin based upon cytological analysis and apparent morphological similarities to both S. pectinata and S. patens. The cytological data presented by Church show identical chromosome numbers for the species involved. S. pectinata from New England was shown to have a somatic number of 42, identical to that found for the putative hybrid. From these data he concluded that crossing must have occurred between S. pectinata and the hexaploid segment of the S. patens population. While this hexaploid segment has been considered taxonomically separable from the tetraploid, evidence presented below in connection with S. patens shows that the two are not at all discrete, but that they grade imperceptibly into one another so as to defy separation. Similarly, within S. pectinata, the existence of a series of polyploids, not morphologically separable from one another, is reported.

In an effort to test the validity of Church's hybrid hypothesis a hybrid index was constructed according to methods described earlier in connection with S. longispica (page 502). Because the polyploids within each parent species are not morphologically separable from one another, all available specimens of both parents were used to ascertain ranges of variability in the characters utilized. The discussions of those characters possessing measurable variability are accompanied by tables showing the range of variability within both the parent species. The total number of specimens of each species introduced into the tables will be seen to vary from table to table. This variation occurs because certain structures were missing on some of the specimens. Many more specimens were used in assessing variability than were eventually scored by means of the hybrid index because some specimens, otherwise perfectly identifiable, did not possess all the morphological parts necessary for complete scoring.

The hybrid appears to have only a sporadic distribution along the east coast of the United States from New Hampshire to Maryland. Accordingly, only specimens from this particular region were used to determine ranges of variability within the parent populations. The twenty characters used in constructing the hybrid indes are presented below:

1. The rhizomes in S. pectinata are thick and hard, possessing closely imbricated cales. Those of S. patens are thin and wiry with scales scarcely imbricate. An intermediate condition was not found. The hybrids either do not possess rhizomes or have rhizomes resembling those of S. pectinata. In cases where rhizomes are wanting, the intermediate index value of 1 is assigned.

2. The rhizomes of S. pectinata are distinctly brownish-purple in color while those of S. patens are whitish. Again, as in the preceding feature, the rhizomes of the hybrids, when present, are like those of S. pectinata. In instances where rhizomes are wanting, an index value of 1 is assigned.

3. Table 6 shows the distribution of flowering culm heights for specimens examined. Preliminary investigations in the hybrid swarm showed that heights of culms averaged about 1 meter. Accordingly, all specimens which were found in the range of overlap (81--120 cm) between the parents were assigned the index value of 1.

Table 6. Distribution of Culm Heights by Classes

Distribution classes (cm)	S. pectinata	S. patens	S. X caespitosa
0--10	0	0	0
11--20	0	2	0
21--30	0	18	0
31--40	0	40	0
41--50	0	29	0
51--60	0	28	0
61--70	0	20	2
71--80	0	17	6
81--90	0	12	5
91--100	3	3	6
101--110	2	1	6
111--120	9	6	5
121--130	3	0	4
131--140	11	0	0
141--150	5	0	0
151--160	6	0	0
161--170	1	0	0
171--180	0	0	0
181--190	2	0	0
191--200	0	0	0
201--210	0	0	0
211--220	0	0	0
221--230	1	0	0
231--240	0	0	0

4. The leaf blades of S. pectinata are usually flat, becoming involute toward the apex. Those of S. patens are commonly involute throughout. An intermediate condition was not discernible.

Table 7. Distribution of Second Blade Widths and Lengths by Classes

Distribution Classes	*S. pectinata*	*S. patens*	*S. X caespitosa*
	Second Blade Widths		
0--0.9 mm	0	65	0
1--1.9	0	67	0
2--2.9	0	27	7
3--3.9	0	6	11
4--4.9	0	3	13
5--5.9	2	0	1
6--6.9	8	2	2
7--7.9	23	0	0
8--8.9	10	0	0
9--9.9	11	0	0
10--10.9	8	0	0
11--11.9	1	0	0
12--12.9	3	0	0
13--13.9	1	0	0
	Second Blade Lengths		
0--3.9 cm	0	0	0
4--7.9	0	28	0
8--11.9	0	49	1
12--15.9	0	32	1
16--19.9	0	14	2
20--23.9	0	18	7
24--27.9	0	8	5
28--31.9	0	3	7
32--35.9	1	3	4
36--39.9	4	1	2
40--43.9	3	0	2
44--47.9	1	0	0
48--51.9	7	0	1
52--55.9	7	0	2
56--59.9	5	0	0
60--63.9	5	0	0
64--67.9	8	0	0
68--71.9	3	0	0
72--75.9	2	0	0
76--79.9	0	0	0
80--83.9	0	0	0
84--87.9	2	0	0
88--91.9	1	0	0
92--95.9	1	0	0

5. Leaf width in the putative parents shows considerable variation. Table 7 shows the distribution of leaf width in the specimens examined. All specimens in the range 4--6 mm were scored with the intermediate value of 1. Measurements were made on the second leaf from the summit.

6. Length of the blades does not separate the parents discretely. However, Table 7 shows that considerable difference exists between the species with respect to blade length. All specimens in the range 24--39.9 cm were assigned the intermediate value of 1. Measurements were made on the second leaf from the summit.

7. Length of the ligule serves to separate the parent species discretely. Ligules in S. pectinata vary from 1--3 mm. S. patens has ligules which rarely exceed 0.5 mm. Those specimens with ligules exceeding 0.5 mm but less than 1 mm were assigned the intermediate value of 1.

Table 8. Distribution of Panicle Lengths by Classes

Distribution classes (cm)	S. pectinata	S. patens	S. X caespitosa
0--1.9	0	0	0
2--3.9	0	4	0
4--5.9	0	32	0
6--7.9	0	47	0
8--9.9	0	29	3
10--11.9	0	19	4
12--13.9	0	21	3
14--15.9	0	20	7
16--17.9	1	3	8
18--19.9	2	5	5
20--21.9	6	3	3
22--23.9	8	0	1
24--25.9	11	0	0
26--27.9	11	0	0
28--29.9	10	0	0
30--31.9	15	0	0
32--33.9	7	0	0
34--35.9	11	0	0
36--37.9	4	0	0
38--39.9	2	0	0
40--41.9	0	0	0
42--43.9	1	0	0

8. Considerable difference in panicle length is evident between the parent species. Panicles in S. pectinata vary from 16--44 cm in length, while those of S. patens range from 2--22 cm in length. Table 8 shows the distribution of panicle lengths in both species. Specimens with panicle lengths within the range of 16--22 cm were assigned a value of 1.

9. Table 9 shows the distribution of spike numbers in both parent species. In cases where spike number was 7--9, these specimens were assigned a value of 1.

Table 9. Distribution of Spike Numbers by Classes

Distribution classes	S. pectinata	S. patens	S. X caespitosa
1	0	1	0
2	0	76	0
3	0	52	4
4	0	24	11
5	0	19	8
6	0	6	2
7	3	3	5
8	5	0	2
9	6	1	2
10	5	1	0
11	9	0	0
12	7	0	0
13	9	0	0
14	8	0	0
15	7	0	0
16	5	0	0
17	4	0	0
18	4	0	0
19	4	0	0
20	3	0	0
21	1	0	0
22	3	0	0
23	3	0	0
24	0	0	0
25	0	0	0
26	3	0	0
27	3	0	0

10. Mean spike lengths of the two parent species differ somewhat although the variability within the specimens examined shows some overlap. Consequently, delimitation of an intermediate does not seem advisable here. Table 10 shows the distribution of spike lengths for each parent species. A value of 55 mm was selected as an arbitrary division point. Accordingly, specimens with spike lengths of 55 mm or less (typical of S. patens) were assigned the index value of 2, while those exceeding 55 mm (typical of S. pectinata) were givan a value of 0.

Table 10. Distribution of Spike Lengths by Classes

Distribution classes (mm)	S. pectinata	S. patens	S. X caespitosa
0--5	0	0	0
6--10	0	0	0
11--15	0	1	0
16--20	0	4	0
21--25	0	19	0
26--30	0	28	0
31--35	0	32	1
36--40	0	19	6
41--45	2	20	6
46--50	2	21	4
51--55	3	10	4
56--60	5	9	5
61--65	8	2	4
66--70	10	3	2
71--75	10	1	2
76--80	10	1	0
81--85	14	0	0
86--90	8	0	0
91--95	7	0	0
96--100	2	0	0
101--105	2	0	0
106--110	0	0	0
111--115	1	0	0
116--120	2	0	0
121--125	2	0	0
126--130	0	0	0
131--135	0	0	0
136--140	1	0	0

11. Peduncle lengths appear to differ significantly between the two parent species. Lengths of the peduncles of median spikes in S. patens were not found in excess of 5 mm while the value in S. pectinata commonly exceed 5 mm. No intermediate was defined here. The hybrids exhibited considerable variability in this respect.

12. Longer spikelets with a range of 11--21 mm appear to be more typical of S. pectinata while shorter spikelets with a range of 6--14.9 mm characterize S. patens. Data presented in Table 11 show an overlap between 11 and 14.9 mm. Consequently, any spikelet having a length within that intermediate range was assigned a value of 1.

Table 11. Distribution of Spikelet Lengths by Classes

Distribution classes (mm)	S. pectinata	S. patens	S. X caespitosa
6--6.9	0	3	0
7--7.9	0	20	0
8--8.9	0	40	0
9--9.9	0	50	0
10--10.9	0	28	4
11--11.9	2	17	7
12--12.9	3	7	9
13--13.9	7	3	4
14--14.9	9	2	6
15--15.9	12	0	3
16--16.9	20	0	0
17--17.9	13	0	1
18--18.9	11	0	0
19--19.9	8	0	0
20--20.9	2	0	0
21--21.9	1	0	0
22--22.9	0	0	0
23--23.9	0	0	0
24--24.9	0	0	0
25--25.9	0	0	0
26--26.9	1	0	0

13. The first glume of S. patens is commonly shorter than one-half the length of the second glume. In contrast, first glumes of S. pectinata are almost always longer than one-half the length of the second. Only in cases where the length of the first glume was found to be exactly one-ha f that of the second was the intermediate value of 1 assigned.

14. Considerable difference in length of first glumes was found between the parents. Table 12 shows variation from 2--5 mm for S. patens and from 5--12 mm for S. pectinata. Values from 5--5.9 mm are assigned the intermediate value of 1.

Table 12. Distribution of First Glume Lengths by Classes

Distribution classes (mm)	S. pectinata	S. patens	S. X caespitosa
2--2.9	0	5	0
3--3.9	0	36	1
4--4.9	0	19	6
5--5.9	2	1	15
6--6.9	10	0	8
7--7.9	13	0	4
8--8.9	17	0	0
9--9.9	14	0	0
10--10.9	7	0	0
11--11.9	2	0	0
12--12.9	2	0	0

15. The tip of the first glume in S. pectinata is typically awned, while that of S. patens is merely acuminate. Because of the difficulty in determining how much of the tip is actually awn, no intermediate was defined here.

16. As with the preceding, the same differences are noted between the parents with respect to the tip of the second glume.

17. The second glume of S. pectinata is typically 1--3-nerved. When three nerves are evident, the two lateral nerves are disposed, one on either side of the prominent mid-nerve (keel). S. patens second glumes are 3-nerved and the two lateral nerves are both disposed on only one side of the prominently pubescent mid-nerve (keel).

18. Pubescence on the keel of the second glume in S. pectinata is very strongly pectinate while that of S. patens is hispid.

19. As with the preceding, the same differences are noted between the parents with respect to pubescence on the keel on the lemma.

20. The tip of the lemma in S. pectinata is bilobed and each lobe is distinctly acuminate, while in S. patens the tip is obtuse, rounded or obscurely bilobed (Plate V, j-m).

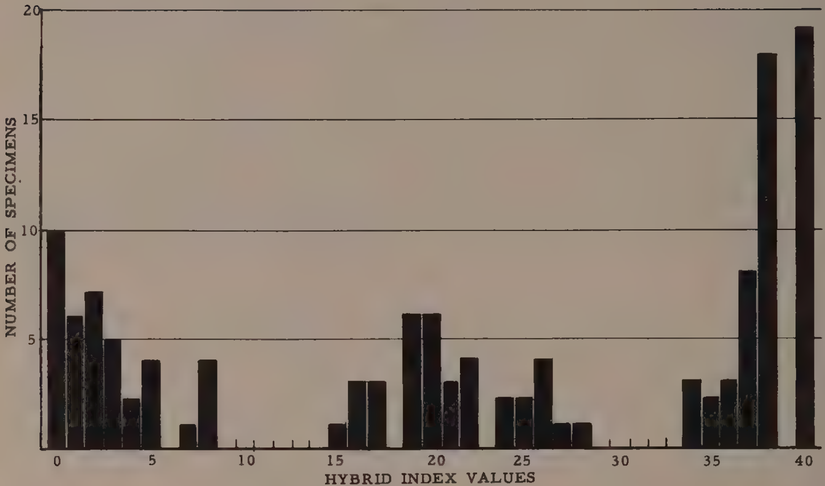

Fig. 11. Distribution of Hybrid Index Total Scores

Results of the scoring of 128 specimens are shown in Fig. 10. The putative hybrids are represented by the intermediate cluster, values 15 to 28. It appears from the data presented that the hypothesis of hybrid origin of S. caespitosa is further substantiated.

For items 3, 5, 6, 8, 9, 10, 12, and 14, tables are presented which show the variability within the putative parent populations. After the scoring of parents and hybrids was completed, measurement date from plants of the hybrid swarm were tabulated. These data are shown in the fourth column of each of the tables.

While the intermediate specimens appear to be members of a population which is discrete from either putative parent, there exists within this intermediate cluster considerable variability especially with regard to rhizomes. Field observations show that the plants without extensive rhizomes grow in large, dense caespitose clumps often as much as 50 cm across. From observations on herbarium specimens which fall within the intermediate cluster on Fig. 11. but possess extensive rhizomes, it appears that the plants do not have a true caespitose habit. Quite to the contrary, they appear to arise as solitary upright culms, much as in S. pectinata. Certain plants of caespitose habit were observed to possess occasional short rhizomes in addition to the numerous, short, extravaginal shoots.

As Blomquist (1948) has suggested, perhaps the caespitose habit may be merely an ecological form. However, field observations do not bear this conclusion out. A visit to the type locality, an abandoned seaside pasture one mile east of the town of Seabrook, New Hampshire, proved quite rewarding. At that station, S. caespitosa of the true caespitose habit was found abundantly. Growing very near it on the same disturbed soil were large numbers of rhizome-producing specimens of S. pectinata

and S. patens. If the production of rhizomes was a mere response to environmental conditions, one would certainly have expected to find rhizomatous S. caespitosa at that station. That only the caespitose form occurs there was borne out by extensive observations that required the uprooting of virtually every clump of S. caespitosa in the immediate vicinity.

A more likely explanation for the variability of underground structures is that hybridization between S. pectinata and S. patens may occur repeatedly and that the capacity for rhizome production may be controlled by hereditary mechanisms. Certainly, conditions favoring hybridization are present throughout the known range of S. caespitosa. The flowering periods of the putative parents are coincident. They grow in the same habitat, often together, and they both vary with regard to polyploidy These factors, coupled with the results of scoring by means of the hybrid index and the sporadic distribution, lend considerable support to the hypothesis that the intermediate plants are actually members of a polyphyletic hybrid swarm standing intermediate between S. patens and S. pectinata. That crossing of the putative parents does produce viable seeds has been demonstrated experimentally by Church (1940). However, his seeds failed to develop beyond the seedling stage.

If such crosses be of frequent natural occurrence, opportunity might be offered for a rather wide variety of character segregation. The genetic mechanisms which may control the production of rhizomes are not known, but it is entirely possible that such mechanisms may account for the variability evident in regard to the rhizomes.

The true caespitose forms may themselves be polyphyletic. The fact that some caespitose clumps seem to produce rhizomes might indicate that a separate cross was involved in their formation.

Among the clumps examined at the type locality, a distinct difference was noted in one. It was unlike any of the others in that its leaves were completely involute, quite as leaves of S. patens, while the others possessed flat leaves more typical of S. pectinata. The presence of this unique clone may further indicate that hybridization is of frequent occurrence. These specimens (Mobberley 249, ISC) are very similar to the type specimens of Eaton.

Further evidence supporting that polyphyletic origin theory may be found in the differences manifested by the hybrid specimens in regard to certain features typical of the putative parents. For example, the character in item 17 of the hybrid index above is perfectly stable for each parent, but the hybrids vary considerably, some resembling S. patens, others S. pectinata. While there is no evidence supporting a view that the hybrid population is capable of maintaining itself by breeding true, field observations indicate that the caespitose form without rhizomes is capable of extensive vegetative reproduction. Several clumps distributed across a small abandoned dump at the type locality are virtually identical. Considerable vegetative reproduction is evident in the caespitose clumps themselves where new culms are seen to arise from the many short, extra-vaginal shoots.

While the hybrid swarm doubtless has some difficulty increasing its distribution in competition with its more aggressive congeners, there appears to be little doubt that it is persistent.

Nomenclature

The species was first described by Eaton (1898) from a specimen collected in a seaside pasture near Seabrook, New Hampshire. The type specimen is of the caespitose form and shows no evidence of rhizomes.

Hitchcock (1906) reduced the species to S. patens var. caespitosa on the grounds that it was identical with S. patens except for the caespitose habit. However, as shown in the hybrid index above, S. patens and S. caespitosa are separable on more counts than simple habit. Eaton's type, upon which Hitchcock's variety was based, was scored according to the hybrid index and was found to have a total score of 21.

Fernald (1950), having seen morphological features which obviously related S. caespitosa to both S. patens and S. pectinata, reduced the species to a hybrid category. Evidence presented above would appear to support the hybrid hypothesis, but it is apparent that the members of the hybrid swarm are not all of the same ancestry. In accordance with

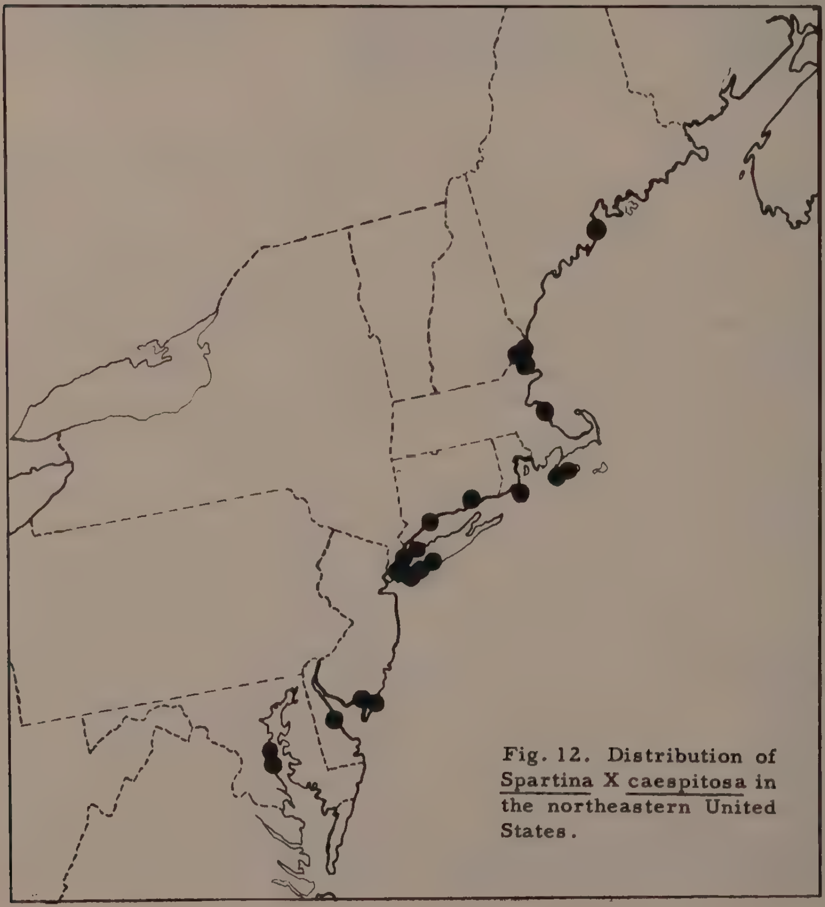

Fig. 12. Distribution of Spartina X caespitosa in the northeastern United States.

Article H. 1 of the International Code of Botanical Nomenclature (1952), the hybrid swarm is designated Spartina X caespitosa until more information is available. It may be possible to show that individual segments of the hybrid swarm are capable of maintaining themselves as discrete taxonomic entities and might therefore be regarded as distinct species.

Distribution

Fig. 12. shows the distribution of specimens examined. Specimens referable to the hybrid swarm by means of the hybrid index seem to occur only where the ranges of S. pectinata and S. patens are coincident.

That Spartina X caespitosa grows in the same habitat as its putative parents is significant. The habitats are mostly the drier portions of salt and brackish marshes, in areas some distance above the intertidal zone. At the type locality, clumps of the hybrid were found within 50 feet of the water's edge at high tide. Perhaps the most significant feature concerning this hybrid is that it was not found on any but disturbed soil. At the type locality, the part of the seaside pasture in which these plants were found had obviously been used as a dump, for the author encountered all sorts of household refuse during the collection of underground portions of the caespitose clumps. None of the hybrids were found on ground that had not been disturbed, although the parents seemed to flourish on this dump as well as on the undisturbed ground nearby. An illuminating note is appended to the label on a hybrid specimen (Eames 4071, Bridgeport, Conn., GH) to the effect that the specimens was collected from "made ground" at the edge of a salt marsh. The prevalence of a number of intermediate specimens in and near New York City, where little if any ground has likely remained undisturbed, might be considered further evidence supporting the hybrid hypothesis. As Anderson (1949) has pointed out, the success of naturally occurring hybrids seems to be enhanced when the environment particular to the parent species is in some way disturbed.

12. SPARTINA CYNOSUROIDES

Spartina cynosuroides (L.) Roth. Cat. Bot. 3:10. (1806)
Dactylis cynosuroides L. Sp. Pl. ed.1. 71. (1753)
(Type in BM from Virginia)
Trachynotia polystachya Michx. Fl. Bor. Amer. 1:64. (1803)
(Type in P from South Carolina)
Limnetis polystachia Rich. in Pers. Syn. Pl. 1:72. (807)
Spartina cynosuroides (L.) Willd. Enum. Pl. 81. (1809) pro parte.
Spartina polystachya (Michx.) Beauv. Nouv. Agrost. 25. (1812)
Cynodon cynosuroides (L.) Rasp. Ann. Sci. Nat. Paris I. 5:303. (1825)
Spartina cynosuroides Willd. var. polystachya (Willd.) Scribn. Bull. Torrey Club. 10:86. (1883)
Spartina cynosuroides (L.) Roth var. polystachya (Michx.) Beal ex Fern. Rhod. 49:113. (1947)

Description (Plate IV, e-h)

Culms to 3.5 meters tall, erect, stout, terete, glabrous, solitary from stout, widely spreading rhizomes, scales closely imbricate; sheaths smooth to striate, the lower often wrinkled, glabrous, the margin of the orifice often densely pilose; ligule a ring of hairs 1--3 mm long; blades elongate, flattened, glabrous on both surfaces, margins scabrous, tip acuminate; panicle 15--40 cm long; panicle axis 3--4-angled, prominently contorted on the more robust specimens, glabrous to scabrous on the angles; spikes 5--67, 6--15 cm long, alternately to irregularly arranged, spreading, occasionally appressed, imbricate, sessile or pedunculate, the peduncles as much as 4.5 cm long; rachis of the spikes glabrous to scabrous on the angles; spikelets 10--70, 9--14 mm long, alternate, tightly appressed, closely imbricate; first glume linear, 3--7 mm long, usually less than one-half the length of the second, glabrous, keel strongly hispid, margins hispidulous, tip acute; second glume 9--14 mm long, glabrous to hispidulous, keel hispid, lateral nerves prominent, one on either side of the keel, nerves hispid, margins of the glume hispidulous, tip acuminate; lemma glabrous to sparingly hispidulous, often only on the upper half, keel hispid, tip obtuse or rounded; palea thin and papery, often hispidulous near the summit of the keel, tip acuminate, exceeding the lemma; anthers 4--6 mm long; somatic chromosome numbers 28, 42.

Observations

S. cynosuroides is a rather uniform species, although less robust plants may resemble, superficially at least, vigorous specimens of S. patens. The plant is essentially a coarse halophyte which was observed to reach a height of 3.5 meters in one locality (Pungo, Va. Mobberley 209, ISC). The vegetative parts of the plant, in general, exhibit much more vigor than similar parts in the other species within this complex. Considerable variation was found in measured values for certain vegetative parts commonly used as key characters. Ligule length was found to be quite variable, not differing significantly in this respect from most other species of Spartina.

The more important characteristics from the standpoint of plant identification are spike number, spike length, peduncle length, spikelet length, relative glume lengths, and tips of glumes and lemmas.

Reports concerning spike number in this species are somewhat at variance. Fernald (1947, 1950) states that in the maritime variety, up to 100 spikes may occur on a single panicle. However, during the examination of over three hundred panicles from across the range of distribution, the greatest number of spikes encountered on any one panicle was sixty-seven. On the other hand, Small (1933) reported the maximum number of spikes to be about fifty. This value is shown to be slightly less than the number encountered in specimens collected by the author from southeastern United States.

A character of this species which appears to be of some taxonomic significance is the position of the nerves on the second glume. Two lateral nerves are usually prominent, one on either side of the keel. Very often the lateral nerves are hispid. This character is illustrated in Plate IV, f.

Two specimens (Chapman, Fla. MO) geographically identified only as "Florida" are almost completely glabrous along nerves and keels of all parts of the spikelet (Plate IV, h). However, this feature is not sharply delimited, for a number of specimens, particularly those from the Gulf Coast area, show a tendency to be less copiously hispid than others from more northerly stations.

One chromosome count has been previously reported. Church (1940) found this species to have the hexaploid number of 42 from a station in East Dennis, Massachusetts. During the present investigation, chromosome numbers of both 28 and 42 were found. These findings are presented in Table 13.

Table 13. Chromosome Numbers in S. cynosuroides

Mobberley 55	Cypremort Point, Louisiana	2n = 42
Mobberley 158	St. Mary's, Georgia	2n = 28

Plants found to have the tetraploid number of chromosomes were critically compared with the hexaploids. No morphological differences were found that would permit a satisfactory taxonomic separation of the two. Differences may exist in certain anatomical features wuch as guard cell size, epidermal cells, and the like. However, these were not studied during the present investigation. Not nearly enough specimens with chromosome numbers known are available to make a more satisfactory disposition of the apparent differing levels of polyploidy.

Nomenclature

This species, named by Linnaeus (1753) as Dactylis cynosuroides, was based upon a plant collected in Virginia by Clayton. The original description was that of Gronovius (1743). Linnaeus gave this plant the specific epithet cynosuroides and appended a variety β which is clearly identified as S. alterniflora. Subsequently, a number of European authors, among them Loefling (1758) and Michaux (1803), took up the specific epithet and applied it mistakenly to other species within the genus. Loefling misapplied the epithet to the European S. maritima and Michaux to the American S. pectinata. Michaux then settled on the epithet polystachya for the present species.

Richard (1807), apparently without the knowledge of Schreber's earlier description of Spartina, transferred Michaux's Trachynotia and the spartinoid segment of Linnaeus' Dactylis to the genus Limnetis. Limnetis polystachia was obviously an orthographic variant of Limnetis polystachya. Hitchcock (1953) gives Limnetis cynosuroides in synonomy for Spartina cynosuroides, but it appears that Limnetis cynosuroides of Richard is actually Michaux's Trachynotia cynosuroides, now shown to be a synonym of Spartina pectinata.

Roth (1806) correctly identified the true cynosuroides of Linnaeus with the genus Spartina. His combination seems to merit recognition as the valid one. Roth does not cite polystachya at all and thus it remained for Beauvois (1812) to effect the transfer of Trachynotia polystachya to Spartina. It stands now as a synonym of S. cynosuroides.

Scribner (1888) concluded upon examination of several anomalous spikelets that the present species was merely a variety of the more widely distributed transcontinental S. cynosuroides Willd. The erroneous usage of the epithet cynosuroides for S. pectinata is reviewed in connection with the synonomy of that species. Scribner held that because some spikelets of the more southern coarse halophyte were found with atypically long first glumes, the entire species should be regarded as a variety.

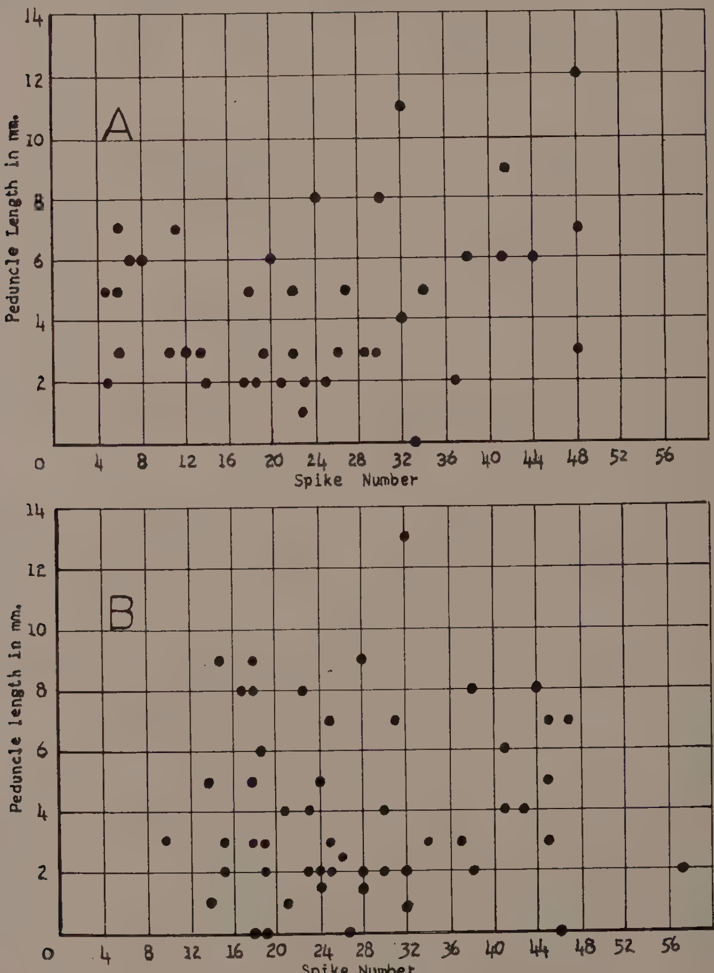

Fig. 13. Comparison of Specimens of Spartina cynosuroides from Maritime and Brackish Water Habitats by Spike Number and Peduncle Length.

A. Maritime Habitat. B. Brackish Water Habitat.

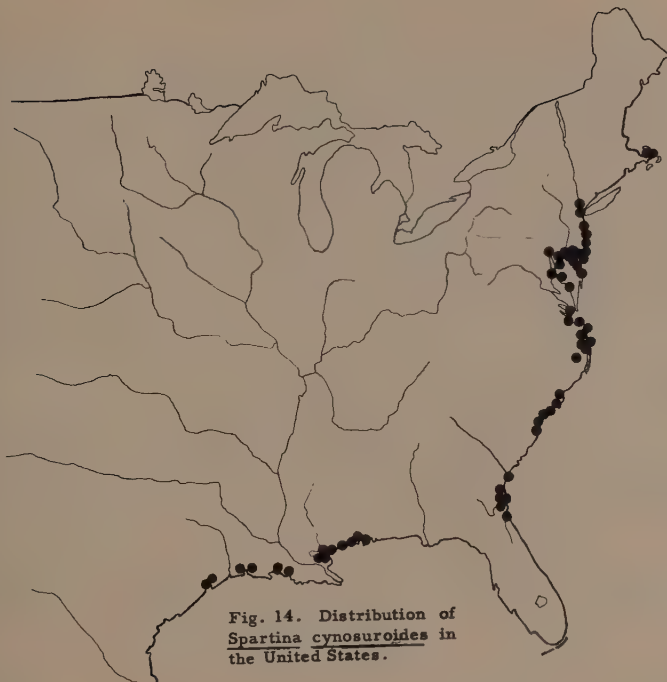

Fig. 14. Distribution of Spartina cynosuroides in the United States.

Beal (1896) favored Scribner's varietal rank for the present species. However, Fernald (1947) used Spartina cynosuroides (L.) Roth var. polystachya (Michx.) Beal to name what he regarded as a distinct variety of the southern halophyte. Fernald sought to distinguish var. polystachya from the typical variety on the basis of its exclusively maritime habit, and 30--100 short-pedunculate to subsessile spikes. The typical variety is supposed to have 6--50 spikes, longer peduncles (no values are given) and a fresh to·brackish water habitat.

Fernald's observations were made principally in Princess Anne County, Virginia, where he found the two varieties supposedly quite selective of habitat. He also quotes Bayard Long to the effect that the two varieties are similarly disposed in New Jersey, Delaware, and eastern Pennsylvania. It is significant to note that Pohl (1947) in the most recent treatment of Pennsylvania grasses does not cite the present species as occurring anywhere in Pennsylvania. Chase (1950) states that habitat is not satisfactorily correlated with morphological distinctions.

In an effort to determine whether the variety is actually distinct from the typical form, extensive collections from both brackish water and maritime habitats were made by the author, particularly in Princess Anne County, Virginia. The collections were studied from the standpoint of spike number and peduncle lengths. Peduncle measurements were made on a median spike. Results of the investigation are presented in Fig. 13, where spike number is plotted against peduncle length. Two

diagrams were constructed, one for fresh to brackish water plants and the other for strictly maritime plants.

The scatter diagram shows that scarcely one-third of the maritime specimens examined answered to Fernald's spike number criterion. Many specimens with fewer than 30 spikes were found in maritime habitats. The diagram also shows that a considerable number of plants of brackish to fresh water habitat possess peduncles much shorter than those found on many of the strictly maritime specimens. The failure of dots, each representing a single specimen, to become segregated into two discrete clusters would seem to cast doubt upon the presence of two distinguishable populations. In view of the foregoing evidence, it appears desirable to regard the varietal name as a synonym of S. cynosuroides.

Distribution

Distribution of Spartina cynosuroides is shown in Fig. 14. While the plant has been observed in strictly maritime habitats bordering the strand and intertidal zones, the primary habitats seem to be the edges of brackish water estuaries and borders of tidal lagoons and bays. A particularly favored site for the species is the margin of the intercoastal waterway. Collection dates indicate that the plant flowers from June to October. Quite in contrast to the more succulent S. alterniflora, the inflorescence of this species is remarkably free from insect predation, doubtless because of the harsh, indurate texture of the spikelets.

13. SPARTINA DENSIFLORA

Spartina densiflora Brong. Du Perr. Bot. Voy. Coq. 14. (1829)
(Type in P from Concepción, Chile)
Chauvinia chilensis Steud. Syn. Pl. Glum. 362. (1855)
(Type in P from Concepción, Chile)
Spartina montevidensis Arech. Anal. Mus. Nac. Montevideo. 4:378. (1896) (Type from Rio de La Plata shore in Uruguay)
Spartina patagonica Speg. Rev. Agron. La Plata. 579. (1897)
(Type from Santa Cruz, Argentina)
Spartina densiflora Brong. var. typica St. Y. Cand. 5:74. (1932)
Spartina densiflora Brong. var. typica St. Y. subv. brongniartii St. Y. Cand. 5:74. (1932) (Based on S. densiflora Brong. and Chauvinia chilensis Steud.)
Spartina densiflora Brong. var. typica St. Y. subv. pauper St. Y. Cand. 5:77. (1932) (Based on S. patagonica Speg.)
Spartina juncea Willd. var. montevidensis (Arech.) St. Y. Cand. 5:89. (1932) (Based on S. montevidensis Arech.)
Spartina juncea Willd. var. laxiflora St. Y. Cand. 5:88. (1932)
(Type in G from Jacarehy, Brazil)
Spartina platensis Mez. ex St. Y. Cand. 5:86. (1932) nomen, in obs.

Description (Plate IV, i-k)

Culms to 1.5 meters tall, erect, terete, indurate, glabrous, caespitose from hard knotty bases, rarely with short rhizomes, commonly with short extra-vaginal shoots appressed to the culm; sheaths smooth to

somewhat striate, glabrous, the lower indurate and shining, the upper dull and somewhat striate, margin of the orifice glabrous to moderately pilose; ligule a ring of hairs 1--2 mm long; blades elongate, 3--8 mm wide, involute when fresh, commonly scabrous on the adaxial surface, glabrous on the abaxial, margins scabrous, tip acuminate; panicle 10--30 cm long, 4--8 mm wide; panicle axis 3-angled, scabrous on the angles, often twisted; spikes 2--15, 1--11 cm long, 2--3 mm wide, the longer narrow, the shorter broad and often flattened dorsiventrally, alternate, tightly appressed, moderately imbricate, sessile; rachis of the spikes glabrous to scabrous on the angles, not prolonged beyond the terminal spikelet; spikelets 10--30, 8--14 mm long, 1--2 mm wide, the lower usually the longer, alternate, tightly appressed, moderately to closely imbricate; first glume linear, 4--7 mm long, glabrous to sparingly hispidulous, keel hispidulous, margins glabrous to sparingly hispidulous, tip usually obtuse; second glume 8--14 mm long, sparingly hispidulous, keel hispidulous, margins sparingly hispidulous, tip usually acuminate; lemma minutely hispidulous, keel glabrous below, hispidulous above, tip acuminate to obtuse; palea thin and papery, keel glabrous below, hispidulous above, tip acuminate, exceeding the lemma; anthers 3--5 mm long.

Observations

The above description is based upon herbarium specimens from Chile and Argentina which had previously been referred to S. densiflora and upon specimens from Brazil, Uruguay, and Argentina which had been referred to S. montevidensis.

The vegetative parts of the plant are rather uniform throughout the population. The plants were not found to exceed 150 cm in height on any of the sheets. The only vegetative characters of taxonomic significance are the short, slender, upturned shoots arising from the hard, knotty culm bases. The ligule of this species does not differ significantly from that present in most of its congeners.

The important characters of the inflorescence are lengths of the panicles, spikes and spikelets as well as the number of spikes and spikelets. Chilean specimens commonly referred to S. densiflora are distributed across the range of variation in all features except spike lengths and spike number. These two features will be discussed in connection with geographic distribution.

Several other features were somewhat characteristic for the population but these are of doubtful taxonomic significance. They were, however, useful in connection with studies on the putative hybrid origin of S. longispica. Among these features are the relative lengths of the two glumes, the first generally being shorter than one-half the length of the second. As will be pointed out in the discussion of synonomy, this feature was not found to be consistent, but represents only a general trend in the population. The same thing may be said with regard to the glume tips. Plate IV, i-k, illustrates the more common condition found within the specimens examined. The acuminate tip of the palea, although not entirely consistent among the specimens examined, offers a distinctive feature. Spikelets are always readily disarticulated from the rachis. Perhaps not too much regard should be paid to this as a feature of taxonomic significance, since the condition may depend upon maturity and drying.

Nomenclature

The type specimen upon which the name S. densiflora is based was collected by Du Perry from the vicinity of Concepción, Chile. A fragment, deposited in the U.S. National Herbarium, was examined. Although the type specimen has no basal parts according to Hitchcock's note on the herbarium sheet, spikelet morphology clearly relates the type and the fragment to the original description by Brongniart (1829).

Chauvinia chilensis, described by Steudel (1855) is also based upon a plant collected from the vicinity of Concepción. It is difficult to see why Steudel chose to erect the genus Chauvinia when the type specimen of S. densiflora was accessible to him. From his published descriptions of both nomenclatural elements, the only apparent difference is the size of the plants, Chauvinia being slightly the smaller. Comparison of fragments of the C. chilensis type specimen with those of S. densiflora shows that the two undoubtedly belong to the same taxon.

Descriptions of the type specimen of S. montevidensis by Arechvaleta (1896) show it to be unquestionably S. densiflora. In addition to the description, there is presented a full-page, carefully executed drawing showing that the plant is strikingly similar to S. densiflora. Examination of a number of specimens referred to S. montevidensis shows no clear-cut morphological criterion by which a separation of S. montevidensis from S. densiflora may be effected. Parodi (1919) suggested that S. montevidensis might possibly be nothing but a variety of Brongniart's S. densiflora. Critical study of these specimens reveals nothing that would enable one to separate these plants in such a way that even varietal rank would be justified.

Spegazzini (1897) described a plant from the Argentine territory of Santa Cruz, giving it the name S. patagonica. The description of the plant clearly identifies it as S. densiflora although Parodi (1919) in his treatment of the Chlorideae of Argentina recognizes it as discrete from its several congeners occurring in Argentina.

Parodi's criteria for separating the three species which have, in this paper, been reduced to S. densiflora Brong. are presented in tabular form (Table 14). They are based solely on features of the inflorescence.

Table 14. Criteria for Speciation in Certain Spartinas in Argentina (Parodi, 1919)

Character	S. densiflora	S. patagonica	S. montevidensis
Panicle length	15--20 cm	6--15 cm	15--40 cm
Spike length	3--4 cm	2--4 cm	3--8 cm
Spike number	--	3--6	6--14
Spikelet length	12--13 mm	10--12 mm	10--12 mm
Relative lengths of glumes	1st longer than one-half the 2nd	1st shorter than one-half the 2nd	1st shorter than one-half the 2nd

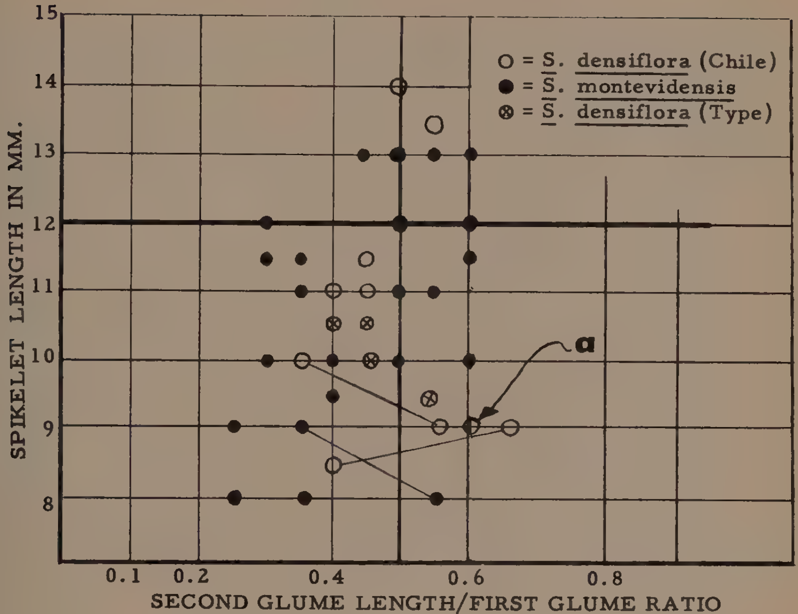

Fig. 15. Comparison of specimens of Spartina densiflora by ratio of second to first glume and spikelet length. ("a" represents a spikelet from the type specimen of Chauvinia chilensis.)

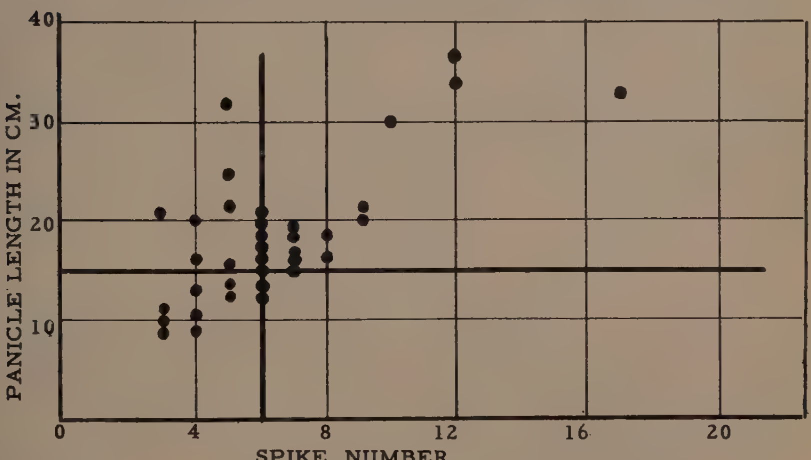

Fig. 16. Comparison of specimens of Spartina densiflora by panicle length and spike number.

It is apparent that S. densiflora should be separable from the other two species on the basis of spikelet length and the ratio of glume lengths. Accordingly, a scatter diagram (Fig. 15) was constructed to learn whether these differences were actually valid and useful. By plotting the numerical value of the ratio of first glume to second glume against the length of the spikelet, it should be possible to show that all the plants examined fall into the first and third quadrants of the diagram, were the criteria valid. However, quite a different picture results. Not only is there a failure of the values to fall into place, but also, in certain situations where more than one spikelet per plant was measured, the scores for two spikelets from the same plant fell into different quadrants. These spikelets are connected by lines on the diagram. In general, an average spikelet was considered to be one from near the middle of a near-median spike. A number of spikelets from the type specimen also were introduced into the diagram. These are marked by an X in the open circles, which show the Chilean specimens. The black dots represent plants referred to S. montevidensis. From the evidence presented, the "species" are not separable from each other on the bases suggested. Further evidence supporting the view that these three "species" are not distinct is presented in Fig. 16, a scatter diagram based upon features which Parodi used to separate S. montevidensis from S. patagonica. By plotting the number of spikes per panicle against the length of the panicle, four quadrants are erected which should have specimens falling into only the first and third, were the criteria valid. Chilean specimens are excluded from this diagram; only specimens previously referred to S. montevidensis were used. No specimens were available which had been referred by others to S. patagonica. The scattering of dots representing specimens throughout all the quadrants but one, and the overlap which appears to exist, suggests that there is little basis for regarding S. patagonica and S. montevidensis as anything but synonyms of S. densiflora.

Saint-Yves (1932) described two subvarieties of S. densiflora var. typica. His variety typica is synonomous with S. densiflora, and, as noted in the discussion of synonomy of S. spartinae, is held by him to be discrete from his variety junciformis which is synonomous with S. spartinae. The two subvarieties of S. densiflora var. typica are separable, according to Saint-Yves, on the basis of the number of spikes and the length of the panicle. His criteria for separating the two taxa are presented in Table 15.

Table 15. Subvarietal criteria within S. densiflora var. typica. Saint-Yves (1932)

	Panicle length	Spike number
S. densiflora var. typica subv. Brongniartii	12--15 cm	12--15
S. densiflora var. typica subv. pauper	10 cm	4--8

Examination of twelve specimens previously identified as *S. densiflora* shows that only four answer the criteria proposed by Saint-Yves (1932). The remainder have panicles in excess of 10 cm in length and fewer than twelve spikes. It is at once apparent that these subvarietal taxa are ill-defined and should accordingly be treated as synonyms of *S. densiflora*.

Spartina montevidensis, shown in this paper to be a synonym of *S. densiflora*, has been considered by Saint-Yves (1932) as *S. juncea* var. *montevidensis* and var. *laxiflora*. His reasons for inclusion of these South American taxa within *S. patens* (*S. juncea*) are not at all clear. The vegetative appearance of *S. montevidensis* is altogether different than that of *S. patens* in that extensive rhizomes, characteristic of *S. patens*, are never found in *S. densiflora*. In addition, spikelets are usually one-nerved in *S. densiflora* and three-nerved in *S. patens*.

The variaties *laxiflora* and *montevidensis* can hardly be considered discrete taxa. *S. juncea* var. *laxiflora* is based upon a specimen collected and identified by P. Dusen as *Spartina alterniflora* Lois. A specimen from the same collection (P. Dusen 14264, MO) was examined. Criteria set up by Saint-Yves for the separation of the two varieties were the lax or gracile appearance of the spikes and the degree of remoteness of the spikelets from one another. Visual inspection of all the plants referred to *S. densiflora* by this author revealed that the lax attitude of the spikes was an extremely variable characteristic occurring occasionally among the specimens examined. Examination of Fig. 7, p. 506, will show that the degree of remoteness of the spikelets when reduced to a numerical basis (ratio of spike length to spike number) is disposed as a unimodal feature across the range of the population sample. The specimen referred to *S. densiflora* var. *laxiflora* occurs near the upper end of the population sample.

Spartina juncea var. *montevidensis* is clearly synonomous with *S. densiflora* for the reasons discussed in connection with the transfer of *S. montevidensis* to *S. densiflora*. This variety is held to be distinct from var. *laxiflora* because of the closely imbricate spikelets and the appressed spikes. As pointed out above, the occasional occurrence of a rather loosely appressed spike is rather sporadic throughout the population sampled, and does not appear to be correlated with other features such as the degree of remoteness of the spikelets. Attempts to delimit the varieties *laxiflora* and *montevidensis* by Saint-Yves are not warranted. All such specimens examined during the course of this study are distinctly referable to *S. densiflora*.

Distribution

S. densiflora is distributed across a considerable area of southern South America. Collection stations are plotted in Fig. 17. A pictorial diagram is attached to each station dot by means of a broken line. The pictorial diagrams show the relative median spike length and spike number of the specimens.

From the description of the species it is evident that considerable variation occurs in the number as well as the length of the spikes. Viewed geographically, a curious fact becomes apparent. Plants with fewer and longer spikes are more or less characteristic of the northern portion of the east coast range. Diminution in spike length and increase in number

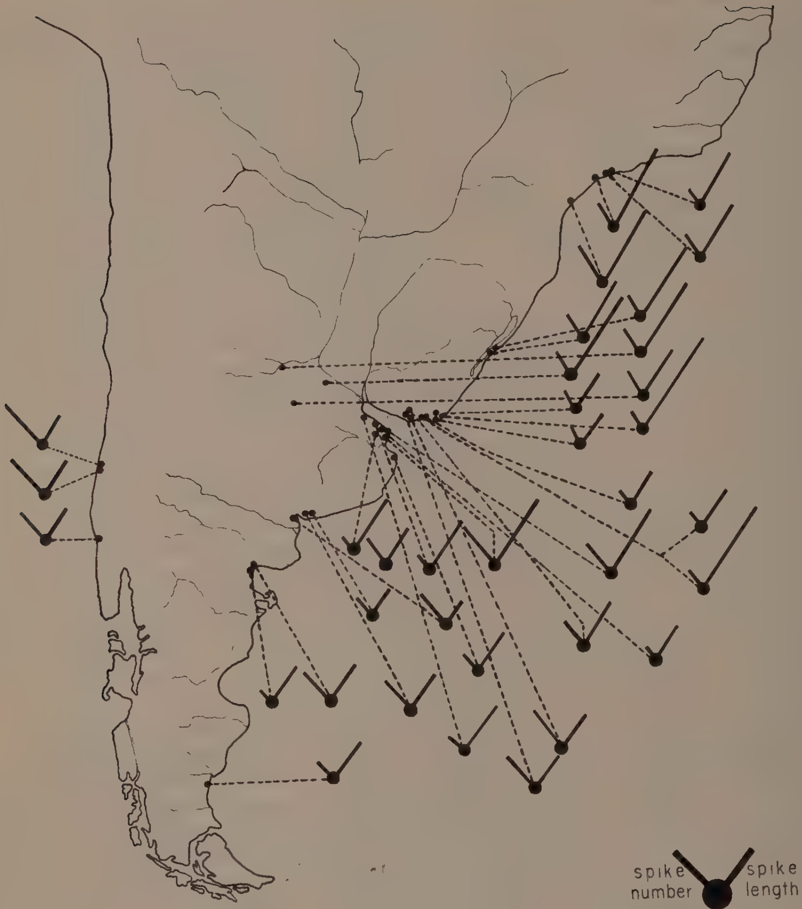

Fig. 17. Distribution of Spartina densiflora in South America. (For discussion of pictorial diagrams, see text.)

are evident as one proceeds southward and across to the coastal areas of Chile. Very often diminution in spike length is accompanied by a perceptible increase in width. These features are not at all consistent but represent only the general trends within the population. In all other characters, no such distribution phenomena were observed. The primary habitat of the species seems to be the drier parts of the coastal marshes. However, several collections have been made at inland stations. Collection records show that the plant flowers from December to May.

14. SPARTINA GRACILIS

Spartina gracilis Trin. Mem. Acad. St. Petrsbg. Sci. Nat. IV. 6:110. (1840) (Type in LE from North America)

Description (Plate V, a-c)

Culms to 1 meter tall, erect, terete, indurate, glabrous, solitary, from widely spreading rhizomes, scales closely imbricate; sheaths smooth to striate, glabrous, the margin of the orifice usually glabrous, rarely short pilose; ligule a ring of hairs 0.5--1 mm long; blades elongate, flat, becoming involute, scabrous on the adaxial surface, glabrous on the abaxial, margins scabrous, tip acuminate; panicle 8--25 cm long; panicle axis 3--4-angled, flattened, scabrous on the angles; spikes 4--12, 1.5--8 cm long, 2--6 mm wide, alternate, usually appressed, not closely imbricate, sessile; rachis of the spikes scabrous on the angles; spikelets 10--30, 6--11 mm long, alternate, appressed, rarely spreading, moderately imbricate; first glume narrow, 3--7 mm long, glabrous to sparingly pilose, keel glabrous to pilose, margins sparingly hispidulous, tip acute or often mucronate; second glume 6--10 mm long, glabrous to sparingly pilose, keel pilose, margins glabrous to sparingly hispidulous, tip awnless, acute or often mucronate; lemma glabrous to sparingly pilose, keel pilose at least on the upper one-half, margins sparingly hispidulous, tip obtuse, rounded or obscurely lobed; palea thin and papery, glabrous, sparingly hispid above, tip obtuse to slightly rounded; anthers 2.5--5 mm long; somatic chromosome number 42.

Observations

This species is one of the more uniform ones within the genus despite the fact that it is distributed from south-central Mexico to the McKenzie Territory in Canada and occurs at altitudes from about sea level in the Great Basin to 7200 feet. Comparison of specimens from widely separated geographic localities shows little variability other than in spike number and culm height. None of the variations could be correlated with geographic distribution. Similarly, comparison of specimens collected at varying altitudes revealed no marked differences. Some variability exists in spikelet shape, grading from ovate to lanceolate (Plate V, a-c), but spikelet shape could not be correlated with other morphological features or geographical or ecological distribution. The ovate spikelets are shorter, in general, than are the lanceolate. The second glumes of the more ovate spikelets may be acute to obtuse at the tip while the more lanceolate are usually acuminate. Of particular importance taxonomically is the presence of two (rarely one) prominent lateral nerves on the second glume. Both are disposed on one side of the densely pilose keel.

A single chromosome count has been reported. Church (1940) found the species to have the hexaploid number of 42.

Nomenclature

A photograph of the type specimen, received from the Komarov Botanical Institute of Leningrad, clearly establishes that Spartina gracilis is properly typified. The photograph is deposited in the herbarium of the Iowa State College.

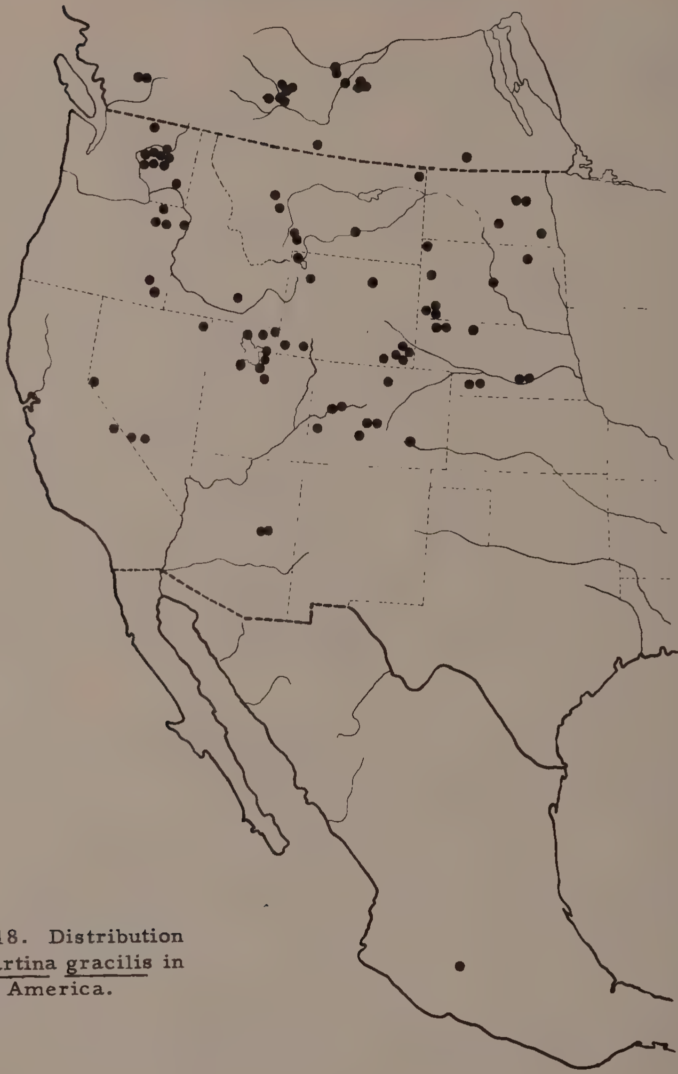

Fig. 18. Distribution of Spartina gracilis in North America.

Distribution

Distribution of this species is shown in Fig. 18. Two specimens collected from the McKenzie Territory north of Saskatchewan have been omitted from the map. These two specimens and the one from Mexico are similar in every respect to the majority from the central portion of the range.

The plants grow in a somewhat specialized habitat, usually at the margins of alkali lakes and along stream margins and river bottoms. The plants flower from June to October.

15. SPARTINA PATENS

Spartina patens (Ait.) Muhl. Descr. Gram. 55. (1817)
Dactylis patens Ait. Hort. Kew. 1:104. (1789) (Type grown in England from seed from New York; isotype in K)
Trachynotia juncea Michx. Fl. Bor. Amer. 1:64. (1803) (Type in P from Carolina)
Limnetis juncea (Michx.) Rich. in Pers. Syn. Pl. 1:72. (1807)
Spartina pumila Roth. Cat. Bot. 3:10. (1806)(Type from New York)
Spartina juncea (Michx.) Willd. Enum. 81. (1809)
Limnetis juncea (Michx.) Rich. var. monogyna M.A. Curtis Bost. Jour. Nat. Hist. 1:136. (1835) (Type from Cape Fear, North Carolina; isotype in GH)
Spartina americana Roth in Trin. Mem. Acad. St. Petrsbrg. Sc. Nat. VI. 6:109. (1840) pro syn.
Spartina duriaei Parl. Fl. Ital. 1:230 (1848)
Spartina versicolor Fabre, Ann. Sci. Nat. Paris III. 13:123. (1849) (Type from Southern France)
Spartina patens (Ait.) Muhl. var. juncea (Michx.) Hitchc. Rhod. 8:210. (1906) (Based on Trachynotia juncea Michx.)
Spartina juncea (Michx.) Willd. var. juncea St.Y. Cand. 5:82. (1932)
Spartina juncea (Michx.) Willd. var. juncea (Michx.) St. Y. subv. europaea St.Y. Cand. 5:82. (1932) (Based on S. duriaei Parl.)
Spartina juncea (Michx.) Willd. var. juncea (Michx.) St. Y. subv. americana St. Y. Cand. 5:84. (1932)(Based on S. juncea Willd.)
Spartina juncea Willd. var. patens (Ait.) St. Y. Cand. 5:86. (1932) (Based on Dactylis patens Ait.)
Spartina patens (Ait.) Muhl. var. monogyna (M. A. Curtis) Fern. Rhod. 49:114. (1947) (Based on Limnetis juncea var. monogyna M.A. Curtis)

Description (Plate V, d-k)

Culms to 1.5 meters tall, slender, erect, terete, glabrous, usually solitary or in small clumps from widely spreading, slender, wiry rhizomes, scales not closely imbricate; sheaths smooth to striate, glabrous, margin of the orifice glabrous, rarely short pilose; ligule a ring of hairs 0.5 mm, rarely to 1 mm long; blades short, involute, rarely flat, narrow, scabrous on the adaxial surface, glabrous on the abaxial, margins scabrous, tip acuminate; panicle 3--15 cm long; panicle axis 3--4-angled, scabrous on the angles; spikes 2--15, 1--7 cm long, alternate, appressed or spreading, often distant, commonly sessile, occasionally pedunculate; rachis of the spikes scabrous on the angles; spikelets 10--30, 7--12 mm long, alternate, tightly appressed, closely imbricate; first glume linear, 3--8 mm long, glabrous to sparingly hispidulous, keel hispid, margins sparingly hispidulous, tip acuminate; second glume 7--12 mm long, glabrous to sparingly hispidulous, keel hispid, lateral nerves commonly hispid, disposed on one side of the keel, margins glabrous to hispidulous, tip acuminate; lemma glabrous to sparingly hispidulous, keel hispid at the tip, margins glabrous to very sparingly hispidulous, tip obtuse, rounded or often obscurely lobed; palea thin and papery, glabrous, tip obtuse, rounded, exceeding the lemma; anthers 3--5 mm long; chromosome numbers 28, 35, 42, 56.

Observations

Spartina patens, a highly variable species, has been found to possess several levels of polyploidy (Church, 1940). Specimens from Massachusetts, Virginia, and Florida were shown to possess the tetraploid, hexaploid, and octoploid number of chromosomes respectively. According to Church, comparison of morphological differences among the specimens showed that the one from Florida was considerably more robust than the others, and the one from Massachusetts had spikelets much less closely imbricate on the spike. The Massachusetts specimen corresponded to S. patens while the Virginia and Florida specimens answered to the description of S. patens var. juncea.

The several specimens whose chromosome numbers were determined as a part of the present investigation do not answer satisfactorily to the descriptions of the two taxa nor do they agree with the geographic distribution of polyploid levels suggested by Church.

Table 16. Chromosome numbers in S. patens

Collection	Location	Chromosome number
Mobberley 115	Fort Walton, Florida	2n = 35
Mobberley 121	Destin, Florida	2n = 42
Mobberley 193	Cape Hatteras, North Carolina	2n = 28

The pentaploid does not seem to be morphologically different from either of the others. It is presumed that it originated from a cross involving tetraploid and hexaploid parents.

Several authors (Fernald 1947, 1950; Hitchcock 1906, 1935; and Merrill 1902) have held the view that this species is distinctly separable into two well-defined taxa. Chase (1950) recognized the two taxa but stated that intermediate specimens occurred frequently. Fernald (1947), having rectified the earlier nomenclatural errors, recognized S. patens and S. patens var. monogyna. The two are supposedly distinguished by a number of morphological criteria, geographic distribution which overlaps somewhat and differing ecological preferences. That occurrence in differing habitats is not correlated with morphological differences will be shown in the section of this paper dealing with distribution.

The several morphological characters by which the two taxa are supposedly separated are tabulated in Table 17.

In some cases, specimens could be assigned to one of the two taxa on the basis of the criteria provided. However, the degree of overlap in most of the criteria precluded the accurate identification of many.

In an effort to learn whether the population was actually divisible into the two taxa suggested, a method of numerical analysis was invoked. The range of variability was determined for each of the above criteria amenable to numerical analysis. These data were accumulated from the examination of 235 specimens. Simple measuring or counting was sufficient for most of the criteria. Blade angle was measured with a protractor in degrees from the longitudinal axis of the culm. Spikelet imbrication was

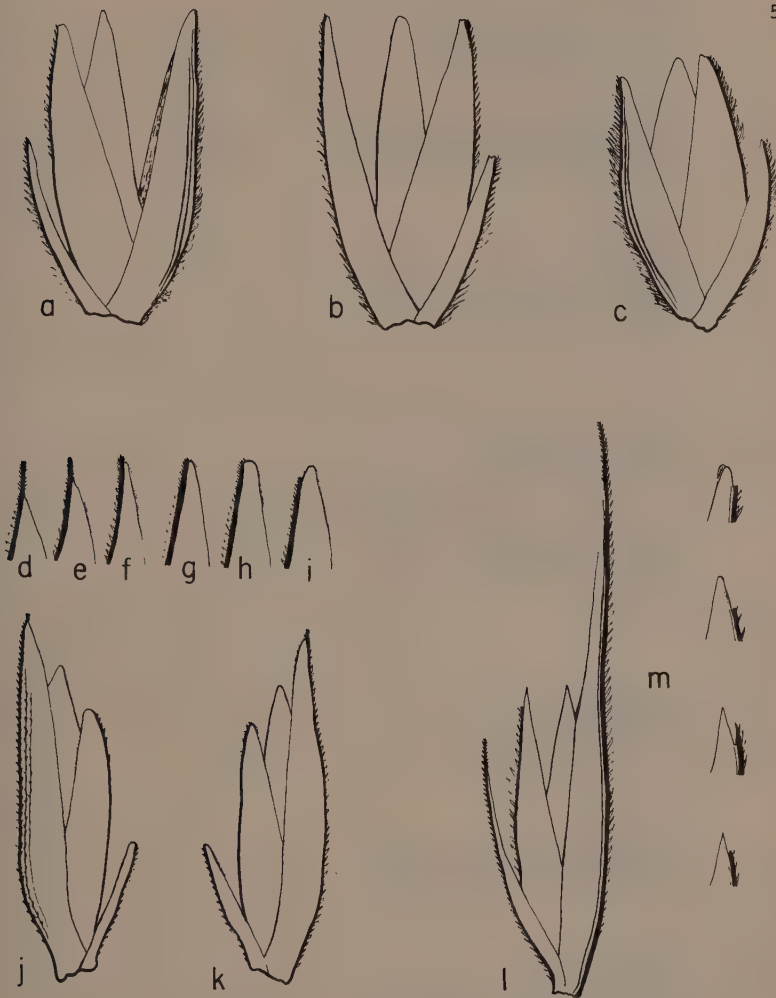

PLATE V

a-c.	Spartina gracilis.	a. spikelet showing lateral nerves 3.75X,
		b. same spikelet, opposite view 3.75X,
		c. spikelet, 3.75X.
d-k.	Spartina patens.	d-i. variation in second glume tips 7.5X,
		j. spikelet showing lateral nerves 3.75X,
		k. same spikelet, opposite view 3.75X.
l-m.	Spartina pectinata.	l. spikelet 3.75X,
		m. variation in lemma tips 7.5X.

Table 17. Criteria of Merrill (1902) and Fernald (1950) for separating S. patens from var. monogyna

Character	S. patens	S. patens var. monogyna
Rhizome diameter (mm)	1--3	2--6
Culm diameter (mm)	1--2.5	1--6
Culm height (dm)	1.5--8	2--15
Leaf number	2--5	5--9
Blade length (dm)	0.5--2	1--5
Blade angle	spreading	appressed
Spike number	1--4	2--9
Spikelet length (mm)	9--13	7--10
Spikelet imbrication	loose	tight
Second glume tip	acuminate	acute to blunt

reduced to numerical terms simply by dividing spikelet number into spike length. The second glume tip was found to vary considerably, grading from acuminate (nearly aristate) to blunt. Its range of variability was arbitrarily broken up into six specific types which served as models by which the tips could be numerically scored (Plate V, d-i). Once determined, the range of variability of each character was divided into six classes as shown in Table 18.

Table 18. Class values for morphological criteria of S. patens

Criteria	0	1	2	3	4	5
Rhizome diameter (mm)	0--1	1.1--2	2.1--3	3.1--4	4.1--5	5.1--6
Culm diameter (mm)	0--1	1.1--2	2.1--3	3.1--4	4.1--5	5.1--6
Culm height (cm)	14--36	37--59	60--82	83--105	106--128	129--150
Leaf number	3--4	5	6	7	8	9--12
Blade length (cm)	3--8	9--14	15--20	21--26	27--32	33--41
Leaf blade angle	77--65°	64--52°	51--39°	38--26°	25--13°	12--0°
Spike number	1--2	3	4	5--6	7--9	10--13
Spikelet length (mm)	11--14	10--10.9	9--9.9	8--8.9	7--7.9	5--6.9
Spikelet imbrication value	2.7--3.4	2.3--2.6	1.9--2.2	1.5--1.8	1.1--1.4	0.7--1.0
Second glume tip	Pl. V, d	Pl. V, e	Pl. V, f	Pl. V, g	Pl. V, h	Pl. V, i

The values are arranged so that classes zero and five characterize typical S. patens and var. monogyna, respectively. Distribution by classes for each of the ten characters is shown in Fig. 19. In all the characters the distribution is unimodal.

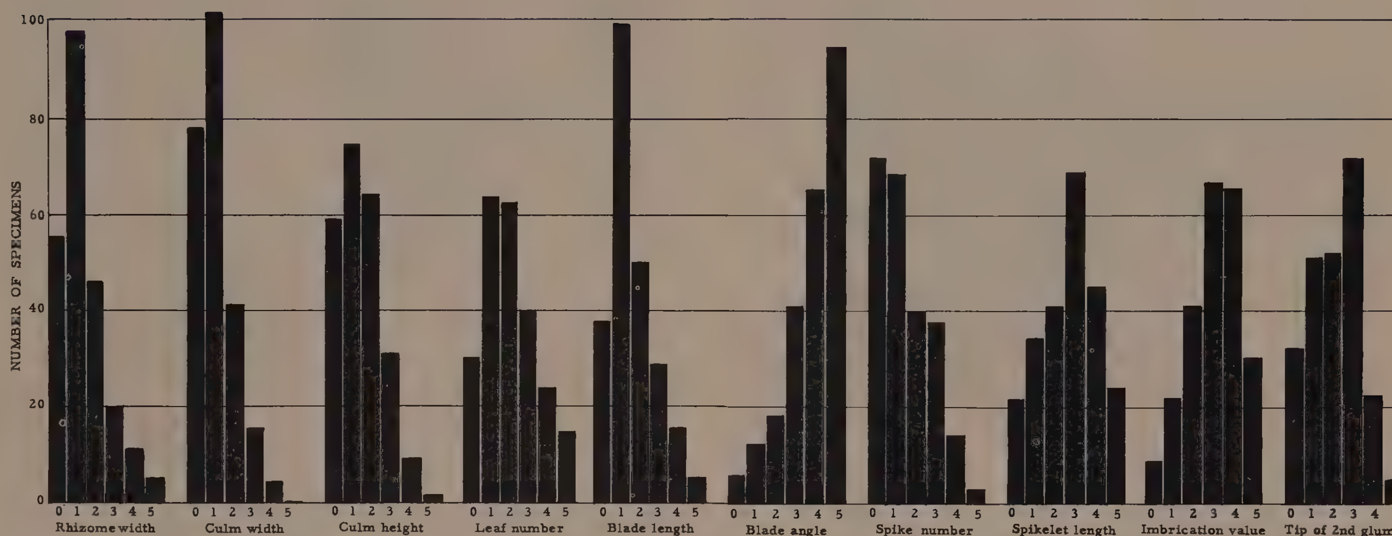

Fig. 19. Distribution by classes (0--5) for morphological features of *Spartina patens*.

Each of the specimens was scored according to the values shown in the above table. The scores for all characters of each specimen were summed and the total introduced into a histogram (Fig. 21). Specimens scored on these bases do not fall into two separable groups.

Fernald (1947) suggested that plants from the region north of New Hampshire were the typical S. patens and that plants south of Virginia were variety monogyna. The distribution of the two taxa was thought to be coincident from New Hampshire to Virginia. None of the criteria utilized in the present study exhibited variability that could be correlated with geographic distribution beyond the fact that smaller plants appear to be more typical of the northern part of the range. However, when the total scores for the specimens were introduced into histograms in which the three geographic sections of the range were treated independently, some differences in the population became evident. Fig. 21, A, B, and C show that higher total scores were found among specimens from Texas to North Carolina while the lower total scores were found among specimens from Maine northward. However, the large degree of overlap provided by total scores of specimens from the intermediate region and the slight overlap between the southern and northern extremes seem to preclude taxonomic separation.

Seven European specimens were scored according to the methods described above. The total scores for these specimens ranged from twenty-eight to thirty-three. These specimens are not separable from the North American material on the basis of the above criteria.

Nomenclature

Spartina patens was first described by Aiton (1789) as Dactylis patens. The type specimen was not seen. However, Aiton's detailed description offers evidence supporting the accuracy of typification. Muhlenberg (1817) properly effected the transfer of this species to Spartina.

Curtis (1835) recognized two taxa within the species. Limnetis juncea var. monogyna was held to be distinct from L. juncea which he evidently took to be a less robust form. Hitchcock (1906) also recognized two taxa and provided the name Spartina patens var. juncea for the more robust form of the species. Realizing that var. monogyna should have received priority, Fernald (1947) provided the combination S. patens var. monogyna. In the light of the evidence presented above, effective separation of the two taxa is not possible. It therefore seems desirable to regard the entire population as a single species that possesses several indistinguishable levels of polyploidy.

In the recent monographic treatment of the genus Spartina by Saint-Yves (1932), this species was subdivided into varietal and subvarietal categories under the name Spartina juncea. The segment of Saint-Yves' S. juncea recognized as S. patens in this paper was subdivided into var. patens and var. juncea. The latter, in turn, was subdivided into subv. americana and subv. europaea. Variety juncea was held to be separable from variety patens by virtue of a difference in spike number (three or more in juncea, three or less in patens) and appressed or spreading blades. The present investigation shows that many plants with less than three spikes have leaf blades tightly appressed to the culm. The subvarieties of var. juncea were claimed by Saint-Yves to be separable on

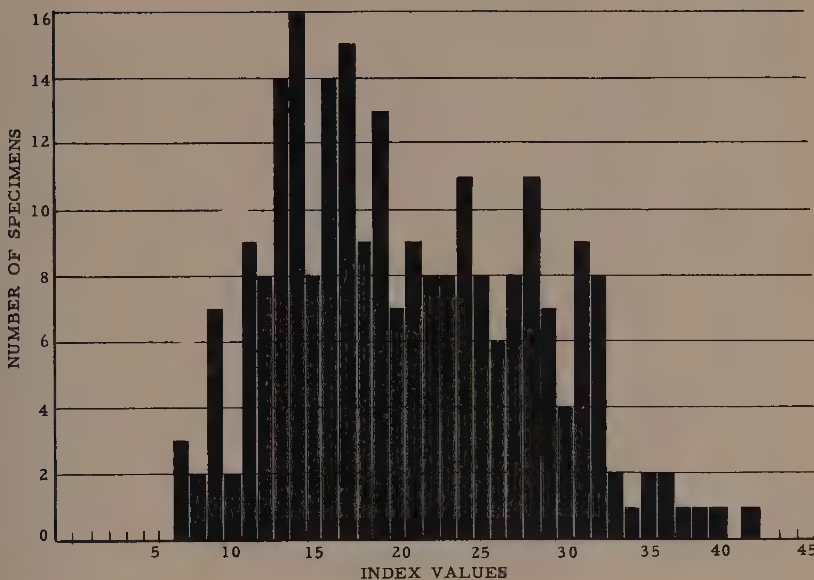

Fig. 20. Distribution of Index Total Scores.

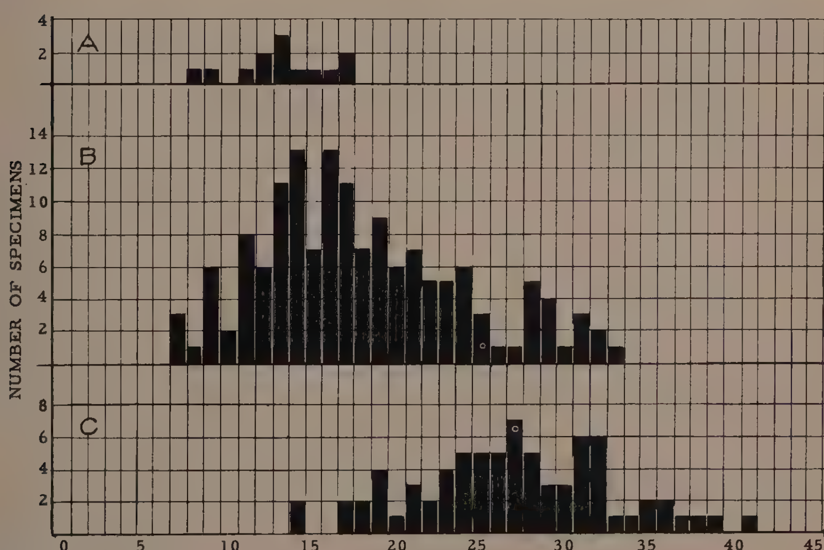

Fig. 21. Distribution of Index Total Scores for specimens of differing geographic localities.
A. Maine to the Maritime Provinces.
B. Virginia to New Hampshire C. Texas to New Hampshire.

Fig. 22. Distribution of Spartina patens in North America and the Caribbean.

the basis of spikelet length which was found to be 6 mm or less in var. europaea and 7--9 mm in var. americana. The present study shows that spikelets of American material may be less than 6 mm in length. Five of the seven European specimens examined have spikelets in excess of 6.5 mm. In view of the obstacles to accurate identification of plants by means of the criteria provided by Saint-Yves, and in the light of the results of the investigation presented in the preceding section, these varieties and subvarietal names are regarded as synonyms of S. patens.

Distribution

Distribution of Spartina patens in North America is shown in Fig. 21. The presence of this species in Europe is probably a result of introduction of rhizomes or seeds from North America by means of ship ballast. It is known from southern France, Corsica, and Italy. A distribution map is not provided for the species in Europe because geographic data on all but one of the sheets were too meager for accurate location of the sites.

While principally a denizen of the coastal salt and brackish water habitats in North America, the species has been found in inland regions in New York and Michigan. These plants from the inland stations are doubtless relics of a maritima flora once common in the Great Lakes region.

Typically, the species is one of the dominant components of the coastal salt marshes. It is frequently found in unbroken stands from the dry, sandy beach above the intertidal zone well up into the drier portions of the marshes. No consistent visible differences could be found in plants that had been collected from the beaches and those from the salt marshes. Occasionally, plants from the beach zone were found to be somewhat glaucous. However, the presence of the bloom could not be correlated with the other morphological characters by which Fernald (1947) sought to set apart S. patens of the salt marshes from S. patens var. monogyna of the strand.

While the time of blooming is somewhat erratic, flowering usually occurs from June to September.

16. SPARTINA PECTINATA

Spartina pectinata Link, Jahrb. Gewachsk. I. 3:92. (1820)
(Type from North America in B)
Trachynotia cynosuroides Michx. Fl. Bor. Amer. 1:64. (1803)
(Not D. cynosuroides of Linnaeus) (Type in P from Illinois)
Limnetis cynosuroides Rich. in Pers. Syn. Pl. 1:72. (1807)
(Based on T. cynosuroides Michx.)
Spartina pectinata Bosc. Ind. Kew. 2:952. (1895) (nomen; error for S. pectinata Link)
Spartina michauxiana Hitchc. Contr. U.S. Nat. Herb. 12:153. (1908)
(Based on T. cynosuroides Michx.)
Spartina michauxiana var. suttiei Farw. Rep. Mich. Acad. 21:352. (1920) (Type in BLH from Orchard Lake, Michigan)
Spartina michauxiana var. tenuoir Farw. Rep. Mich. Acad. 21:352. (1920) (Type in BLH from River Rouge, Michigan)

Spartina cynosuroides Willd. var. michauxiana St.Y. Cand. 5:58. (1932) (Based on T. cynosuroides Michx.)
Spartina cynosuroides Willd. var. michauxiana f. major St.Y. Cand. 5:62. (1932) (Based on S. pectinata Link)
Spartina cynosuroides X gracilis St.Y. Cand. 5:66. (1932) Type not designated; based upon four specimens from Cusick 221, Oregon, 1890. Ballard's Landing, Snake River (error for 2221 in 1899)
Spartina pectinata Link var. suttiei (Farw.) Fern. Rhod. 35:260. (1933) (Based on S. michauxiana var. suttiei Farw.)

Description (Plate V, l-m)

Culms to 2.5 meters tall, erect, terete, indurate, usually solitary from widely spreading, elongate, indurate, brownish rhizomes, scales closely imbricate; sheaths smooth to slightly striate, often keeled above, glabrous, margins glabrous to scabrous, margin of the orifice often pilose; ligule a ring of hairs 1--3 mm long; blades flat, becoming involute in drying, glabrous on both surfaces, margin scabrous, tip acuminate; panicle 10--50 cm long; panicle axis 3-angled, glabrous to scabrous on the angles; spikes 5--50, 1.5--15 cm long, the lower usually slightly the longer, 2--15 mm wide, appressed to somewhat spreading, mostly pedunculate, occasionally sessile, alternately to irregularly arranged; rachis of the spikes glabrous to scabrous on the angles, not prolonged beyond the terminal spikelet; spikelets 10--80, 10--25 mm long, alternate, appressed, closely imbricate, rarely subremote; first glume narrow, 5--10 mm long, glabrous to sparingly hispidulous, keel hispid, tip awned; second glume 10--25 mm long, including the awn, glabrous to sparingly hispidulous, keel pectinate, tip produced into a scabrous awn up to 8 mm in length; lemma glabrous, keel glabrous below, pectinate above, margins hispidulous, tip apiculate, deeply bilobed; palea thin and papery, bilobed and rounded at the tip, slightly exceeding the lemma; anthers 4--6 mm long; somatic chromosome numbers 42, 70, 84.

Observations

Spartina pectinata is a variable species that has been shown to possess at least three levels of polyploidy. Church (1940) reported a hexaploid from Massachusetts and a dodecaploid from Nebraska. In the present investigation, a hexaploid and a decaploid were found from two stations in Iowa.

Table 19. Somatic chromosome numbers for S. pectinata

Collection	Location	Chromosome number
Mobberley 7	Boone County, Iowa	2n = 42
Morrill, John B.	Monona County, Iowa	2n = 70

A comparison of the two specimens shows very little morphological difference. In fact, a comparison of over one hundred specimens from across the range of distribution of the species reveals nothing that would in any way suggest morphological differences that might be correlated

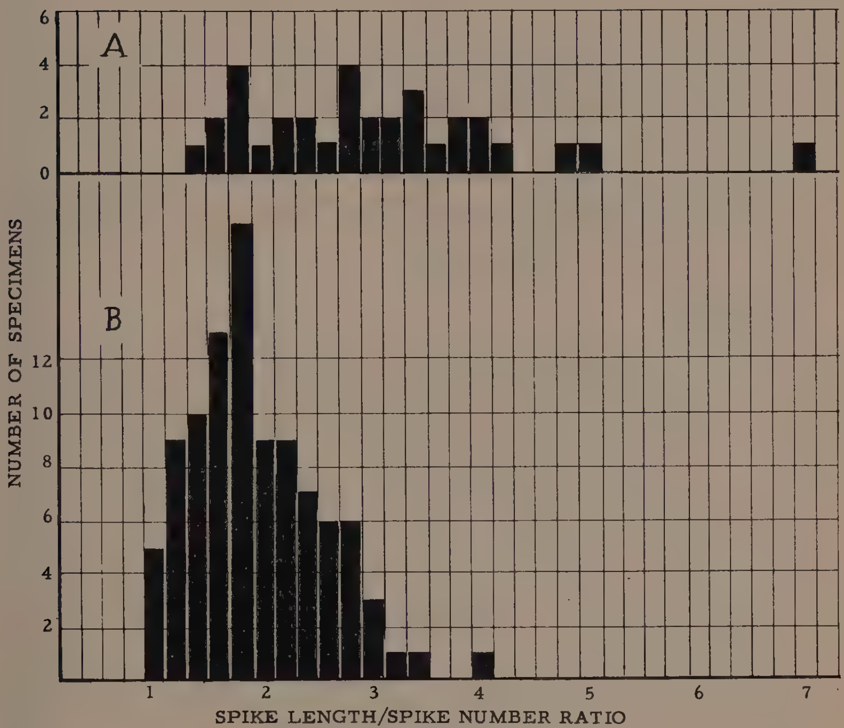

Fig. 23. Comparison of specimens of Spartina pectinata from Eastern and midwestern North America by Spikelet imbrication value. A. Eastern North America. B. Midwestern North America.

with varying levels of polyploidy. A number of specimens were found that had spikelets less closely imbricate along the spike rachis. These specimens seemed to be much more common in material from the maritime provinces of Canada and New England. The imbrication values of a number of specimens were plotted in the accompanying histogram (Fig. 23). The values for specimens from New England and eastern Canada show a much greater variability than do those of the remainder of the range, but nothing in the data presented would enable one to effect a satisfactory taxonomic separation.

The vegetative features of the species offer very little that is taxonomically useful. However, several excellent characters are found in the inflorescence. The extremely long awn, the sharply toothed lemma and the nature of the pubescence are all found useful for separating this species from others of the genus.

Two minor forms of S. pectinata have been described. Irving (1905) published a description for S. cynosuroides (Willd.) var. aureo-marginata. The plant agrees in all particulars with S. pectinata except that the margins of the leaves are striped with a golden band running the length of the

the leaf. It appears that this unusual color form arose as a mutation from an otherwise typical clone. In keeping with the most recent interpretations of taxonomic hierarchy, the variety thus described is reduced to a form and becomes Spartina pectinata Link forma aureo-marginata (Ilv.) comb. nov.

A second such form was described by Marie-Victorin (1944). It differs from the preceding in that the leaves are marked with white along the margins and the median nerve. The type specimen is deposited in the herbarium of Montreal University. Nomenclaturally, it is Spartina pectinata Link forma variegata M.-Vict.

Nomenclature

The case for ascription of the name S. pectinata to the present taxon is carefully stated by Fernald (1933). The first description is that of Link (1820) from a plant sent to him from North America by Bosc. In the original paper, Link cites "Nord-Amerika" as the type locality.

The authors of Index Kewensis (Hooker and Jackson, 1895) have erroneously ascribed the name S. pectinata to Bosc. Fernald (1933) showed that Link's use of the word "von" (S. pectinata, von Bosc) was not a citation of a description by Bosc but was intended only to show that his (Link's) description was based upon a specimen supplied by Bosc. Fernald states that a fragment of the type in the Gray Herbarium, given to Asa Gray many years ago, agrees in all particulars with this present transcontinental species. Thus, there can be little doubt of the validity of the name and the correctness of the author citation.

Considerable confusion has arisen concerning the name Spartina cynosuroides Willd. Correctly cited by Willdenow (1809) in synonomy of the true S. cynosuroides is Dactylis cynosuroides of Linnaeus. Incorrectly cited, however, is Trachynotia cynosuroides of Michaux which has been shown to be synonomous with S. pectinata Link. Michaux (1803) published a description of Trachynotia cynosuroides erroneously basing the specific epithet upon D. cynosuroides of Linnaeus. The plant he described, however, was collected in Illinois and belongs to the inland species; in reality, the true S. pectinata. At the same time, Michaux also described the coarse halophytic species, now known as S. cynosuroides (L.) Roth, as Trachynotia polystachya.

The citation of Michaux's T. cynosuroides by Willdenow undoubtedly led later workers into erroneous usage of the combination S. cynosuroides Willd. or S. cynosuroides (L.) Willd. for S. pectinata. Among those presumably misled by Willdenow and Michaux was Asa Gray (1848). The first edition of The Manual of Botany incorrectly referred the transcontinental inland species to S. cynosuroides Willd. The proper combination was used in a succeeding edition for the first time by Fernald (1950).

Hitchcock (1908) rejected the name S. pectinata on the grounds that the type was collected "probably in South Carolina, where (it) does not grow." In its stead he proposed the name Spartina michauxiana, basing it upon Trachynotia cynosuroides of Michaux. There is no indication that Bosc's collecting expedition was limited to South Carolina or that the type specimen was not obtained by Bosc from some other North American source. The plant is known from Virginia and North Carolina, although

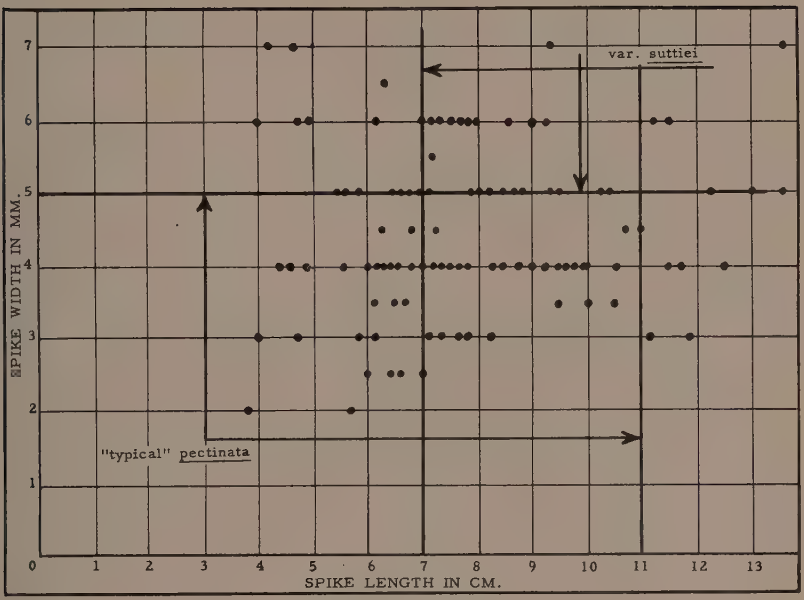

Fig. 24. Comparison of specimens of Spartina pectinata by spike length and spike width.

as Blomquist (1948) has shown, its incidence in North Carolina is restricted to two mountainous localities in the extreme western part of the state.

Several puzzling varieties of S. pectinata have been described. Two of those were published by Farwell (1920) as S. michauxiana var. suttiei and var. tenuior. Holotypes of both of these varieties from the herbarium of the Cranbrook Institute of Science were examined. Varietal rank was assigned the specimens by Farwell on the basis of panicle, spike, and peduncle lengths. Var. suttiei was delimited by panicles 1.5 feet long, spikes 5--7 inches long, and peduncles 1.5--2 inches long. Var. tenuior is delimited by peduncles three-eighths of an inch long or less.

Farwell's variety suttiei does not appear to be separable on the bases offered. Transposed to metric values, the minimum limits for panicle and spike length are 45.7 cm and 12.7 cm, respectively. Of the several hundred panicles of S. pectinata examined during the course of this investigation, only three were found in excess of 45 cm in length, and in each case the median spike length was found to be less than 10 cm. Several specimens were found in which the median spike length exceeded 12.7 cm, but in each ease the panicle length did not exceed 43 cm. The type specimen has a panicle 41 cm long with the median spike 14 cm long. Peduncles in excess of 3.8 cm are supposed to characterize variety suttiei, but of all the specimens examined, only one, a highly aberrant

specimen (Aiton, G.B. 4795, Minneapolis, Minn. WISC), has a peduncle in excess of 3 cm. This specimen had only one elongate spike, the others having aborted. Further, in Farwell's holotype peduncle lengths do not exceed 2.4 cm.

Similarly, Farwell's variety tenuior does not appear to be distinct. In all but one of the features by which Farwell sought to distinguish the variety, it is overlapped by the typical variety. He did, however, set apart variety tenuior on the basis of peduncles which were said not to exceed 0.9 cm. Spikes of the variety were not supposed to exceed 7.5 cm in length. Examination of over one hundred specimens shows that many have spikes in excess of 7.6 cm and peduncles much less than 0.9 cm.

Fernald (1933) took up the variety suttiei and recombined it as S. pectinata Link var. suttiei but ignored Farwell's var. tenuior. This variety is supposedly separable from the typical variety because of its long, narrow spikes. Ranges given for length and width of spikes are: "typical" variety 2--11 cm long, 5--8 mm wide, including the salient awns, var. suttiei 7--15 cm long, 3--5 mm wide. In the variety suttiei the awns are supposed to be appressed and the spikes somewhat more peduncled. No values for peduncle lengths are given. Hitchcock (1935), Swallen (1939), and Chase (1950) all cite this variety as a synonym but state no reasons. Fassett (1951) states that among Wisconsin specimens the spikes vary from 3.5--13 cm in length and from 2--10 mm in width, but that the short spikes are often narrow and the long ones often broad. From this, he concludes that there can be no division of the species into discrete varieties.

In an effort to clarify the picture within this species, spike length is plotted against spike width in a scatter diagram (Fig. 24). Were variety suttiei distinct from the "typical" variety, specimens should fall discretely into the marked sections of the diagram. It appears that instead of a clear-cut separation, dots are found scattered throughout the diagram. The foregoing evidence suggests that both Farwell and Fernald were dealing with selected extremes of a somewhat variable population rather than with discrete infraspecific taxa.

Saint-Yves (1932) described what he thought was an intermediate between S. cynosuroides Willd. and S. gracilis Trin. A type specimen was not designated from among the four specimens of the single Cusick collection 2221 at hand. His description clearly indicates that a somewhat less robust form of S. pectinata is involved. Specimens from this same collection (Cusick 2221, Ballard's Landing, Snake River, Oregon, 1899, F and UC) were examined. There is little doubt that the collection is S. pectinata for the specimens agree in all particulars with that species.

Spartina cynosuroides var. michauxiana f. major has been proposed by Saint-Yves (1932) as an intermediate form between his varieties michauxiana and polystachya. As stated above in the lists of synonyms, the variety polystachya is synonomous with Spartina cynosuroides (L.) Roth, while michauxiana is synonomous with S. pectinata. Saint-Yves seems to have satisfactorily separated his two varieties on the basis of their nearly complete geographic discontinuity. However, plants assigned by him to the intermediate forma major are largely from the range of true S. pectinata and are doubtfully separated from it on the basis of a greater number of spikes. The rather unsatisfactory statement that the two

Fig. 25. Distribution of Spartina pectinata in North America.

varieties grade imperceptibly into one another through the intermediate form concludes his argument. The forma major is therefore referred to S. pectinata as a synonym. That the two "varieties" are discrete species and rather easily separated will be shown in another section of this paper.

Distribution

Distribution of the widely-ranging S. pectinata is shown in Fig. 25. In addition to the stations shown on the map, the species also occurs in a restricted locality at the head of the Adriatic Sea in northern Italy and Trieste. It has presumably been introduced from North America.

The species, in eastern United States and Canada, is an inhabitant of marshes, sloughs, and flood plains. It seems to thrive equally well in both salt and fresh water habitats. Both S. pectinata and S. patens were found in salt marsh habitats in New England often growing intermingled with each other.

In the midwestern United States, S. pectinata has been found in wet

swampy places, but, contrary to most of the statements concerning habitat in extant keys and manuals, the primary habitat seems to be open, dry prarie or high ground along railroad rights-of-way and roadsides. Parcels of native prairie in parts of Iowa show dense growths of this species, often in large, pure stands. That it flourishes on disturbed ground is evident from its abundance on railroad embankments and highway slopes in the Midwest.

In North America, the species flowers from late June to September.

ANALYTICAL KEYS TO THE SPECIES

KEY TO SPECIES OF SPARTINA OCCURRING IN EUROPE AND AFRICA

1. Spikes closely imbricate, several often overlapping; leaf blades over 5 mm wide at the base; spikelets exceeding 10 mm . . 2

1. Spikes not closely imbricate, not overlapping or only the upper part of one spike overlapping the next above; leaf blades less than 5 mm wide at the base; spikelets not exceeding 9 mm in length; western Mediterranean region. . . . . 15. Spartina patens

2. Second glume long-awned, strongly hispid on the keel; culms and rhizomes hard and firm in texture; plants of Trieste and the surrounding region at the head of the Adriatic Sea. 16. Spartina pectinata

2. Second glume not awned, pilose on the keel; culms and rhizomes soft and succulent in texture. 3

3. Spikelets exceeding 15 mm in length. 4

3. Spikelets not exceeding 15 mm in length 5

4. Panicles exceeding 7 mm in width; ligule 1.5--3 mm long. . . . . 9. Spartina townsendii

4. Panicles not exceeding 5 mm in width; ligule about 1 mm long; plants of southwestern France. . . . . 8. Spartina neyrautii

5. Leaf blades readily disarticulating, not exceeding 12 cm · spikelets densely pilose. . . . . 7. Spartina maritima

5. Leaf blades not disarticulating, exceeding 17 cm in length; spikelets not usually densely pilose. 6

6. Rachis of a median spike not less than 1 mm in width; plants of southwestern France. . . . . 8. Spartina neyrautii

6. Rachis of a median spike not more than 1 mm wide; not plants of southwestern France if over 1 mm. 4. Spartina alterniflora

Discussion

The European species of Spartina are not too difficult to identify. The introduced S. patens is easily distinguished from the other European species on the basis of its short spikes and spikelets, densely imbricate spikelets and narrow leaves. S. pectinata, also introduced, may be distinguished from its congeners on the basis of its strongly hispid second glume keel, long awn, and restricted distribution at the head of the Adriatic Sea.

That the introduced S. alterniflora is discrete from the indigenous S. maritima was shown by Fernald (1916), although some earlier authors considered the two identical. Fernald cited the readily disarticulating leaf blades and the fact that the rachis is not prolonged beyond the terminal spikelets as features by which S. maritima differed from S. alterniflora. The disarticulating leaf blades of S. maritima appear to be a constant feature throughout the population, in about one-half of the eighty specimens of S. maritima examined by this investigator, the rachis of the spikes was actually prolonged beyond the terminal spikelet, often by as much as 1 cm.

Jovet (1941) showed that S. alterniflora was distinct from S. maritima on the basis of ligule length. He gives ligule length values as 0.5 mm for S. maritima and 1.0 mm for S. alterniflora. The present investigation revealed considerably more variation than indicated by Jovet. Ligule lengths were not found to exceed 1 mm in S. maritima, while in the European S. alterniflora they varied from 0.7--2 mm.

Length of leaf blade offers an unusually effective means of separation of the two species. Lengths of the blade of the second leaf from the summit in the European S. alterniflora were found to vary from 17 to 44 cm. Frequently, the second leaf blade in S. maritima was missing. In this event, a blade lower down on the culm was measured. In no case was the length of the blade found to exceed 12 cm.

The degree of pubescence on the glumes also serves to separate the two species. The glumes of S. maritima are densely pubescent, while even in the most pilose specimens of S. alterniflora the amount of pubescence is much less than that encountered in S. maritima (Plates II, a-d and III, c-d).

Pubescence on the keel of the lemma seems to merit some attention. European specimens of S. alterniflora were observed to have an essentially glabrous lemma keel while that of S. maritima is pilose at least on the upper two-thirds. The lemma keel of S. alterniflora may possess a few soft trichomes near the tip.

The nature of the second glume tip may also offer an effective taxonomic criterion. While quite variable in both species, there appears to be a rather definite separation of midvein from the lamina of the glume in S. maritima. Usually no such separation is present in S. alterniflora. Plates II, b, and III, c illustrate the variety of second glume tips encountered in both species.

S. alterniflora has not always been considered discrete from S. townsendii. Chevalier (1923) held S. townsendii to be identical with S. glabra var. pilosa of Merrill. Saint-Yves (1932) recognized none of the features by which the two species may be distinguished. Actual lengths of the leaf blades were not found to be a useful key character, but the fact that the

uppermost blade in *S. townsendii* only rarely exceeds the panicle may have some value. In almost all the European specimens of *S. alterniflora* the uppermost leaf blade exceeds the panicle.

Jovet (1941) found that ligule lengths of the two species were quite different. His findings showed a value of about 1 mm for *S. alterniflora* and 2.5 mm for *S. townsendii*. This feature appears to vary somewhat more than Jovet has indicated. Ligule lengths for *S. alterniflora* were found to vary between 0.7--2 mm, while those of *S. townsendii* vary between 1.5--3 mm.

Length of spikelets has been used successfully as a key character. Spikelets of the European *S. alterniflora* do not exceed 15 mm in length, while those of *S. townsendii* are always 16 mm or more in length.

The degree of pubescence on the glumes also serves to separate *S. alterniflora* from *S. townsendii*, which resembles *S. maritima* in this regard. Similarly, comparison of the keel of the lemmas offers a fair degree of differentiation. The lemma keels of *S. townsendii* are characteristically pilose at least on the upper two-thirds, while those of *S. alterniflora* are essentially glabrous except for the few soft trichomes near the tip.

Comparison of anther lengths shows a discrete difference between the two populations. Those of *S. alterniflora* are not found in excess of 6 mm while those of *S. townsendii* exceed 7 mm.

Stapf (1908) used the nature of the second glume tip as a taxonomic key character. He states that the keel of the second glume is not prolonged beyond the glume tip in *S. townsendii* while it is prolonged in *S. maritima* and *S. alterniflora*. Examination of a number of spikelets of *S. townsendii* shows that this feature is not constant. Plate III, g-h show the variety of second glume tips encountered. It is evident that these glume tips are, in a large measure, similar to those of *S. maritima* by virtue of the distinct separation of keel and glume proper. Hence, this feature may be used to separate *S. townsendii* from *S. alterniflora* but not from *S. maritima*.

Separation of *S. townsendii* from *S. maritima* is easily accomplished, however. Spikelets of *S. maritima* do not exceed 15 mm, anthers do not exceed 6 mm, and leaf blades do not exceed 12 cm. On the other hand, spikelets of *S. townsendii* vary from 16--22 mm, anthers are always in excess of 7 mm, and leaf blades exceed 12 cm. Median spikes of specimens of *S. townsendii* examined during the course of this investigation were found to vary from 10--20 cm in length; those of *S. maritima* with three or more spikes per panicle varied between 3--10 cm. In several cases involving the two-spiked *S. maritima*, spike lengths up to 13 cm were found.

Of some taxonomic significance is the length by which the palea exceeds the lemma in *S. townsendii*. This length varies in *S. townsendii* from 1.5--3 mm and in all but two of the twenty-five specimens examined was 2 mm or more. Such lengths measured in the other European species only rarely exceeded 1 mm.

Perhaps the seat of greatest difficulty within the European spartinas is the separation of *S. neyrautii* from the other species. It has a number of characteristics typical of both *S. alterniflora* and *S. maritima*. That it is discrete from *S. maritima* is evident from a comparison of the

leaves. The blade of the second leaf from the apex exceeds 18 cm in length and is not caducous, quite in contrast to that of S. maritima which does not exceed 12 cm and is readily disarticulated from the sheath.

Comparison of S. neyrautii with S. alterniflora shows that they are indeed similar. At first glance it appears that S. neyrautii is somewhat more robust but quantitative evaluation of certain parts of the inflorescence failed to show any discrete differences. Spike and spikelet length are quite variable in both but are predominantly longer in S. neyrautii. Pubescence of the glumes appears to be somewhat more dense in S. neyrautii but this is an extremely unsatisfactory key character. The only feature which was found useful in effecting a separation of these two related species is the width of the rachis of a median spike. Measurements were made on the flattened adaxial surface of the triangular rachis of a median spike at the approximate center of the spike. Since S. neyrautii has such a restricted distribution, it was compared in this respect only with specimens of S. alterniflora from southwestern France. Values of rachis widths in S. alterniflora varied between 0.5--0.9 mm, while those of S. neyrautii were all in excess of 1.3 mm.

Jovet (1941) has shown that the second glume tips of S. neyrautii and S. alterniflora differ somewhat, those of S. neyrautii agreeing for the most part with S. maritima and S. townsendii. However, the variability encountered in the course of this investigation shows this feature to be a rather unsatisfactory key character. Second glume tips for S. neyrautii are shown in Plate III, e-f. The ligule of S. neyrautii is about 1 mm in length and does not differ significantly from that found in S. alterniflora.

With the exception of panicle width and ligule length, no other characters were found that would enable one to separate S. neyrautii from S. townsendii. At best, panicle width is a rather unsatisfactory criterion since it depends to a large extent upon the degree of appression of the spikelets. Spikelets of S. townsendii showed some variation in this respect. A number of specimens with distinctly spreading spikelets were encountered as were some with spikelets rather tightly appressed. Spikelets of S. neyrautii were found to be tightly appressed. The ligule length in S. neyrautii appears to be quite variable in that values from 0.7--1.3 mm were found. In contrast those of S. townsendii vary from 1.5--3 mm in length. Since ligule length has been shown to vary considerably throughout the genus, diagnosis on this feature alone does not seem advisable.

Perhaps geographic separation is the simplest way in which identification may be made. The two species are not known to overlap as yet, although S. townsendii has shown startling abilities in the matter of migration and subsequent establishment.

KEY TO SPECIES OF SPARTINA OCCURRING IN SOUTH AMERICA

1. Spikes more than 15; panicle spikelike, cylindrical. 2

1. Spikes less than 15; panicle not spikelike, not usually cylindrical. 3

2. Spikelets 8 mm or less in length, lanceolate; panicle narrow, not exceeding 1 cm in diameter; pubescence on glumes and lemmas hispid. . . . . 3. Spartina spartinae

2. Spikelets 8 mm or more in length, ovate; panicle thick, exceeding 1 cm in diameter; pubescence on glumes and lemmas long-pilose. . . . . 2. Spartina ciliata

3. Plants lacking rhizomes; spikelets 8--12 mm in length; pubescence on keels of glumes and lemmas of short, rigid, slender trichomes; spikes usually diminishing in length from base to apex of the panicle. . . . . . 13. Spartina densiflora

3. Plants with rhizomes; spikelets usually exceeding 12 mm in length; pubescence on keels of glumes and lemmas of long, soft trichomes, or rarely wanting; spikes usually subequal in length. 4

4. Median spike rachis exceeding 1 mm in width; ratio of spike length to spikelet number usually 3.5--4.5. . 6. Spartina longispica

4. Median spike rachis seldom exceeding 1 mm in width; ratio of spike length to spikelet number usually exceeding 4.5. . . . . 4. Spartina alterniflora

Discussion.

Identification of South American members of the genus may be accomplished with relative ease in most cases. The more uniform of the species found in South America are S. ciliata and S. spartinae. They are easily distinguished from the other species on the bases of numerous short spikes, always in excess of 15 per panicle and not exceeding 8 cm in length. The spikes are densely imbricate and usually twisted, giving the entire panicle a smooth, cylindrical contour. The two species are separable from each other on the basis of spikelet shape and pubescence. Spikelets in S. ciliata are ovate and the keels of glumes and lemmas possess soft trichomes which may exceed 1.0 mm in length. Spikelets of S. spartinae are lanceolate and hispid with rigid trichomes which do not exceed 0.5 mm in length.

S. ciliata appears to be rather closely related to S. arundinacea which occurs on two widely separated island groups in the South Atlantic and Indian Oceans. Superficially, the two are somewhat alike but they are separable on the basis of spikelet shape and pubescence. S. arundinacea has lanceolate spikelets with hispid pubescence.

S. spartinae in South America is rather easily separated from the other

species by virtue of its geographic distribution. Limited to Paraguay and the inland regions of Argentina, its range of distribution is not coincident with that of the other species. While specimens of S. spartinae from South America examined during the course of this study all possessed panicles with spikes in excess of 15, a number of North American specimens were found to have fewer than 15 spikes. It is entirely possible that such depauperate specimens might be found in South America. If this be true, some confusion could result in attempting to distinguish between S. spartinae and S. densiflora. That some confusion did exist is evident from the perfunctory treatment given the two species by Saint-Yves (1932). He considered them only as varieties of a single species, S. densiflora. His separation of S. densiflora varieties typica and junciformis (our S. spartinae) was based upon the cylindrical appearance of S. spartinae and the length of the panicle and spikelet. The cylindrical aspect of the panicle is certainly distinctive for the more typical specimens of S. spartinae, but it is less apparent in panicles with fewer than 20 spikes. S. densiflora, on the other hand, is not typically cylindrical except where a near maximum number (15) of spikes occurs. Saint-Yves further states that the panicle lengths do not exceed 15 cm in S. densiflora and that the spikelets are 10--11 mm in length. On the other hand, in S. spartinae, he sets 20--35 cm as the limits for panicle length and 6--7 mm for spikelet length. Examination of over one hundred specimens shows that these criteria of Saint-Yves are not answered. A specimen of S. spartinae (Rojas 2269, Lima Pora Chaco, Par. US) was observed to possess two panicles, one 14 cm long, and the other 39 cm long.

S. densiflora and S. spartinae, as defined in this paper, can be shown to be separable. The spikelets of S. densiflora are in excess of 8 mm in length, but in none of the South American specimens of S. spartinae were spikelets longer than 7 mm encountered. Further, the pubescence on the keels of glumes and lemmas differs. In S. densiflora, the pubescence on the spikelets is made up of short, rigid, slender trichomes which are about one-half as long as the thicker trichomes of S. spartinae. Most commonly, in S. densiflora, the first glume is slender and about one-half as long as the second. On the other hand, the first glume of S. spartinae is only rarely less than 2 mm shorter than the first.

Perhaps the source of greatest difficulty within the South American species is the separation of S. longispica from S. alterniflora and S. densiflora. That the latter two are discrete and easily identified has been shown in connection with the hybrid index evaluating the hybrid origin of S. longispica. Hard culms, involute leaves, lack of rhizomes and shorter spikelets all serve to aid in distinguishing S. densiflora from the more succulent-culmed, flat-leaved, rhizomatous S. alterniflora with its longer spikelets. On the same bases, S. densiflora seems to be separable from S. longispica.

However, S. longispica is distinguished from S. alterniflora only with considerable difficulty. As noted in the discussion of the hybrid origin of S. longispica, it was observed to be considerably more robust than the related S. alterniflora. While mean values of panicle and leaf length appear to vary significantly (see Table 5), the overlap encountered renders these characters useless as key criteria.

The only feature which seemingly sets S. alterniflora apart from S.

longispica is the width of the rachis. This structural feature may be perfectly satisfactory, but it would seem inadvisable to consider a specimen properly diagnosed on this basis alone. Perhaps evaluation by means of the characters enumerated in the hybrid index offers the most suitable method of identification.

KEY TO SPECIES OF SPARTINA OCCURRING IN NORTH AMERICA

1. Culms soft and fleshy; rhizomes flaccid, the scales closely imbricate and inflated; pubescence when present usually pilose; blades usually flat, glabrous, margins glabrous, occasionally scabrous. 2

1. Culms indurate and firm; rhizomes when present indurate and firm, the scales closely imbricate or remote; pubescence usually hispid (long-pilose in S. gracilis); blades flat or involute, glabrous or scabrous, margins scabrous. 3

2. Median spikes usually less than 5.5 cm in length; glumes commonly curved; spikes tightly appressed and often twisted, usually more crowded toward the apex of the panicle; California and Baja California. . . . . 5. Spartina foliosa

2. Median spikes usually more than 5.5 cm in length; glumes straight; spikes not tightly appressed nor twisted, not more crowded toward the apex of the panicle; eastern North America, introduced in Oregon and Washington. . . . 4. Spartina alterniflora

3. Rhizomes wanting; panicle spikelike; spikes commonly more than 15, densely imbricate, tightly appressed and twisted, giving the panicle a smooth cylindrical contour; spikelets not exceeding 10 mm in length. . . . . 3. Spartina spartinae

3. Rhizomes present or absent; panicle not spikelike nor smoothly cylindrical; spikes few to many, remote or closely imbricate, appressed or spreading; spikelets 5--25 mm in length. . . . 4

4. Second glume with prominent lateral nerves, the nerves all disposed on one side of the keel; spikes fewer than 15; rhizomes when present slender, whitish. 5

4. Second glume with or without prominent lateral nerves, if prominent, the nerves disposed one on either side of the keel; spikes 3--70, rhizomes when present, thick and purplish-brown in color. 8

5. Rhizomes wanting; culms caespitose, in clumps to 1 meter across; culms and sterile shoots arising from hard, knotty bases. 6

5. Rhizomes present; culms usually solitary, occasionally in small clumps of several culms; sterile shoots arising from the rhizomes. 7

6. Culms exceeding 1.3 meters in height; spikes appressed; Florida and Georgia; anthesis usually December to May. . . . . 10. Spartina bakeri

6. Culms less than 1.3 meters tall; spikes spreading; New England to Maryland; anthesis July to October. . . . . 11. Spartina X caespitosa

7. Spikelets ovate to lanceolate, conspicuously ciliate (pilose) on the keels; floret commonly equalling the second glume; spikes appressed; mountains and plains of western North America. . . . . 14. Spartina gracilis

7. Spikelets linear to lanceolate, hispid on the keels; floret shorter than the second glume; spikes spreading, rarely appressed; salt marshes of eastern North America. . . . . 15. Spartina patens

8. Second blade from the summit usually involute, not exceeding 7 mm in width; spikes fewer than 10; rhizomes present or absent. . . . . 11. Spartina X caespitosa

8. Second blade from the summit flat, usually exceeding 7 mm in width; spikes mostly more than 10; rhizomes present. . . . 9

9. Second glume long-awned, strongly pectinate on the keel, glabrous or rarely hispid on the lateral nerves; lemma tip acuminate, sharply bilobed. . . . . 16. Spartina pectinata

9. Second glume not awned, hispid on the keel and usually on the two lateral nerves; lemma tip obtuse or rounded, not sharply bilobed or only shallowly lobed. . . . . . 12. Spartina cynosuroides

Discussion

The North American species of Spartina, in some cases, present rather formidable obstacles to accurate identification. For some of the specimens at hand, the extant keys seem to serve quite well but very often specimens are found which do not answer to key criteria.

Specimens of S. spartinae are rather readily distinguished from other species on the basis of the dense, cylindric inflorescence. However, in cases where the spikes are few in number, this species approaches S. bakeri, S. gracilis, and S. patens, at least superficially. It is, however, immediately distinguished from all of these by the absence of prominent lateral nerves on the second glume. If lateral nerves are at all evident, they are always disposed on opposite sides of the keel. The two or more lateral nerves on second glumes of S. bakeri, S. gracilis, and S. patens are found on one side of the keel.

S. gracilis may be readily separated from the other North American

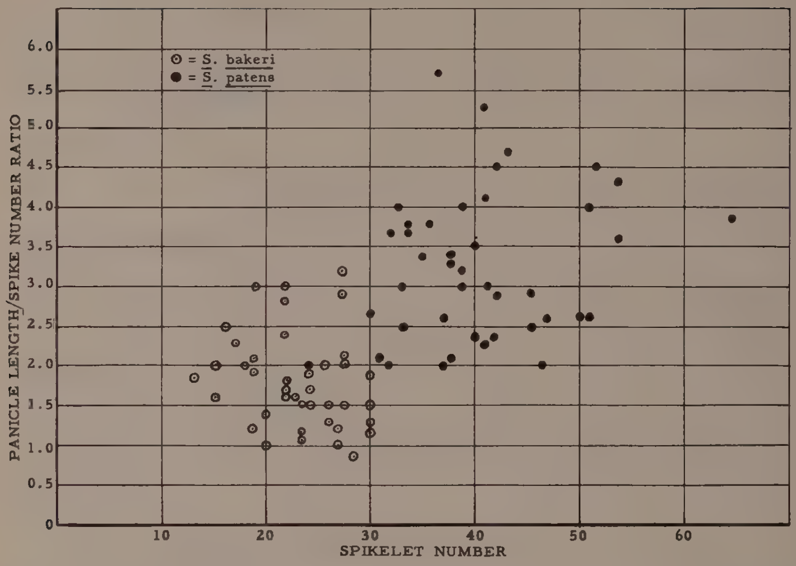

Fig. 26. Comparison of specimens of Spartina bakeri and Spartina patens by ratio of panicle length to spike number and spikelet number.

species by virtue of the copious pubescence in the form of long pilose or villous trichomes. The range of distribution of S. gracilis is coincident only with that of S. pectinata from which it may be distinguished not only by the pubescence but also by the disposition of lateral nerves on the second glume.

A close relationship between S. foliosa and S. alterniflora is suggested by the difficulty encountered in separating them. No single character seems to be perfectly satisfactory. Length of the median spike appears to offer the best criterion, although a median spike length of less than 5.5 cm is characteristic of depauperate specimens of S. alterniflora. Spike number is rarely less than six in S. foliosa. Two of the more than one hundred specimens examined had three elongate spikes. In S. alterniflora, spike number commonly varies from three to fifteen. In S. foliosa, the spikes are noticeably more crowded toward the apex of the panicle; in general, the two lower spikes are somewhat remote. This arrangement of spikes is not particularly evident among specimens of S. alterniflora. The curving of the glumes, especially the first, is a general trend in most of the specimens of S. foliosa examined; this curving was not observed among specimens of S. alterniflora.

Spartina bakeri is completely separable from its congeners only upon the basis of its unique vegetative habit. Very often, information on herbarium sheet labels is lacking concerning this particular feature and recourse must be made to other characters which are taxonomically less certain. The only species with which S. bakeri is likely to be confused

is the highly variable S. patens. Samples of both populations within the geographic range of S. bakeri were studied. Panicle length-spike number ratios were plotted against the number of spikelets from a median spike in Fig. 26. The specimens of S. patens used in the study were largely those of the author's Florida, Georgia, and South Carolina collections, while those of S. bakeri were largely herbarium specimens from the Florida University Herbarium at Gainesville, Florida. Only those specimens of S. bakeri which were satisfactorily identified by means of vegetative habit, time of flowering and geographic location were used in this numerical analysis.

It is evident from the scatter diagram that the two populations tend to differ regarding the characters employed, although some overlap does occur. It should be noted, however, that these criteria hold only for S. patens from the southeastern United States for, as shown in connection with S. patens as a whole, a considerable number of specimens from the more northerly segment of the range possess many fewer than thirty spikelets per spike.

Spartina pectinata is rather readily distinguished from other species of the genus except perhaps S. cynosuroides. These two are somewhat similar and are doubtless closely related. Their range of distribution coincides along the eastern seaboard of North America from Massachusetts south to Delaware. In this area, the two species are usually ecologically segregated. S. cynosuroides inhabits the tidal marshes and lagoons while S. pectinata is ordinarily restricted to the drier parts of the salt marshes, well above the intertidal zone.

Morphologically, the two are found to be separable on several counts. Perhaps the most prominent feature is the awned or aristate second glume of S. pectinata. That of S. cynosuroides is, by contrast, merely acuminate. While it is difficult to draw a fine line of distinction between aristate and acuminate, most specimens of S. pectinata possess enough of an awn to facilitate identification. In the more difficult cases, recourse may be had to several other fairly distinctive character differences. The base of the rachis of the spikes in S. cynosuroides is somewhat contorted and knotty, while that of spikes of S. pectinata is perfectly straight and smooth or scabrous. The lemma tip in S. pectinata is acute, and distinctly bilobed, while that in S. cynosuroides is obtuse or rounded and not markedly bilobed. A comparison of the pubescence on the keels and nerves of the second glumes usually shows a difference. The pubescence is strongly pectinate and usually limited to the keel in S. pectinata. but in S. cynosuroides it is hispid, shorter in length, and distributed along the lateral nerves as well as the keel.

Perhaps the seat of greatest taxonomic difficulty in the North American species concerns S. X caespitosa. Because of its polyphyletic hybrid origin, it exhibits various combinations of Characters of both S. patens and S. pectinata. The absence of rhizomes and the caespitose habit are adequate criteria for distinguishing some members of the hybrid swarm. However, in dealing with those that possess rhizomes, no single character allows a satisfactory separation from the S. pectinata parent. These rhizomatous members of the hybrid swarm may best be identified by evaluation of the characters listed in the hybrid index constructed for S. X caespitosa.

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PUBLICATIONS OF MEMBERS OF THE STAFF OF THE IOWA STATE COLLEGE FOR THE ACADEMIC YEAR 1954-55

Certain summaries and indices are of interest in a survey of the publications of members of the staff of an educational and research institution such as the Iowa State College. The publications are listed in alphabetic order under the names of the senior authors. Junior authors are also listed alphabetically with cross reference to senior author.

SUMMARY

Number of individuals listed.	701
Number of publications.	725
Number of publications with single author	308
Number of publications with joint authorship.	417
Number of departments or fields represented in publications	45
Number of individuals who serve as editors or on the editorial staff of one or more scientific or technical periodicals.	42

The individuals thus serving are:

Ayres, J.C., Ayres, Q.C., Becker, Biester, Bolton, Brozier, Buchanan, Burroughs, Dahm, Davies, A.W., Diehl, Douglas, Dwelle, Eppright, Fassel, Getty, Gilman, Gowen, Graebner, Harris, Hartley, Hazel, Heady, Heath, Heer, Hendrickson, Iverson, Johnson, I.J., Jones, W.P., Kirkham, Keutemeyer, Loomis, Lunden, Parks, W.R., Riecken, Ross, Snedecor, Sprague, Swanson, Tintner, Wenkert, Werkman.

INDEX TO PUBLICATIONS BY DEPARTMENTS OR FIELDS

The numbers which follow the names of the departments refer to the index number of the alphabetic list by authors.

Aeronautical Engineering: Total 1 - Number 511.

Agricultural Engineering: Total 18 - Numbers 7, 11, 67, 103, 104, 149, 266, 284, 285, 341, 400, 401, 402, 403, 557, 598, 664, 680.

Agronomy: Total 92 - Numbers 1, 4a, 31, 63, 72, 81, 91, 92, 170, 215, 237, 255, 257, 267, 268, 269, 270, 271, 303, 304, 335, 342, 343, 349, 365, 366, 374, 391, 406, 418, 419, 426, 436, 437, 438, 452, 453, 457, 458, 459, 505, 514, 520, 548, 549, 550, 551, 552, 578, 582, 583, 584, 585, 588, 589, 590, 594, 595, 596, 602, 605, 606, 607, 608, 621, 622, 638, 639, 640, 641, 646, 647, 654, 662, 663, 665, 680, 683, 684, 686, 694, 697, 698, 699, 700, 701, 702, 703, 704, 717, 718, 719.

Animal Husbandry: Total 38 - Numbers 2, 3, 4, 21, 116,117, 119, 120,121, 122, 123, 124, 125, 126, 127, 130, 131, 177, 216, 321, 353, 354, 409, 412, 439, 449, 476, 477, 478, 479, 502, 506, 507, 564, 572, 595, 681, 722.

Bacteriology: Total 15 - Numbers 94, 95, 96, 97, 98, 99, 100, 101, 102, 140, 141, 259, 260, 467, 534.

Botany: Total 67 - Numbers 20, 34, 42, 43, 44, 73, 75, 91, 92, 129, 159, 172, 182, 217, 218, 220, 240, 241, 242, 253, 254, 262, 298, 307, 310, 312, 335, 341, 384, 390, 391, 395, 396, 408, 420, 469, 470, 472, 488, 489, 490, 491, 515, 529, 561, 566, 597, 604, 617, 618, 619, 620, 621, 622, 655, 658, 668, 669, 697, 698, 699, 700, 701, 702, 703, 704, 720.

Ceramic Engineering: Total 6 - Numbers 150, 524, 705, 706, 707, 708.

Chemical Engineering: Total 17 - Numbers 12, 13, 14, 15, 16, 17, 58, 59, 60, 76, 77, 78, 243, 251, 264, 265, 632.

Chemistry: Total 98 - Numbers 4, 10, 28, 29, 30, 41, 55, 60, 70, 71, 79, 80, 88, 89, 131, 132, 133, 134, 155, 178, 179, 180, 186, 209, 210, 211, 212, 213, 214, 247, 248, 256, 261, 272, 273, 274, 275, 276, 286, 287, 288, 289, 290, 291,

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AUTHOR INDEX

SUBJECT INDEX